DEFINING GENETIC POPULATION STRUCTURE AND HISTORICAL CONNECTIVITY OF SNOW CRAB (*CHIONOECETES OPILIO*)

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DEFINING GENETIC POPULATION STRUCTURE AND HISTORICAL CONNECTIVITY OF SNOW CRAB (*CHIONOECETES OPILIO*)

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Abstract

The snow crab (*Chionoecetes opilio*) is a valuable commercial resource within the Bering Sea, as well as other areas in the North Pacific and Atlantic Oceans. Large populations are known to exist within the Chukchi and Beaufort Seas, including recently discovered commercial sized individuals (Beaufort). However, genetic connectivity throughout these regions has not been examined until now. Based on seven polymorphic microsatellite loci, relatively low population genetic structuring occurs throughout the Alaskan region (G_{ST} = 0.001). This homogeneity is likely due to long-distance larval dispersal, adult migrations, and a possible recent population expansion following the last glacial maximum. Furthermore, meta-population analysis was conducted for Alaskan and Northwest Atlantic stocks. Although significant genetic divergence characterizes the West Greenland stock in relation to all other populations, low divergence (G_{ST} = 0.005) was found between Atlantic Canada crabs and those from the Alaska region. Larval dispersal between regions is highly unlikely due to the transit distance. Therefore, low divergence is likely the result of a recent population expansion into the Northwest Atlantic <5000 years ago.

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Introduction

Snow crab (*Chionoecetes opilio*) occur throughout the continental shelf regions of the N Pacific, NW Atlantic and Arctic Oceans (Fig. 1). The species represents a valuable commercial resource in many regions; however, within the Eastern Bering Sea (EBS) it has historically comprised the largest and most valuable crab fishery in the US (328.6 million pounds harvested in 1991, over $155 million ex-vessel; NPFMC 2010). Snow crab harvest increased during the 1980s (Fig. 2) as catches of its warmer-water relative, the Tanner crab (*C. bairdi*), began to decline. Since that time, the Bering Sea snow crab stock has undergone large fluctuations in population size (Fig. 2) and was declared overfished in 1999 due to low survey estimates of mature crab biomass (NPFMC 2010). A 10-year rebuilding plan was implemented in 2000, and although population estimates have increased since that time, the recovery program has not attained its goal (NPFMC 2010). There are currently no snow crab fisheries in the Alaskan Arctic; however, legal-size snow crab were recently reported in deeper waters (306-478 m) off the Beaufort Sea shelf (Rand and Logerwell 2011), indicating potential for fishery development. Moreover, should the Arctic become increasingly ice-free and open to transit, resource extraction efforts will likely increase. Oil and gas lease sale areas extend over 100 km into the Chukchi and Beaufort Seas from Point Hope to Camden Bay (Fig. 1). These increasing pressures create a need for information on stock structure, genetic connectivity, and spatial dynamics of northern aggregations of snow crab to inform future management efforts.

Harvest of Bering Sea snow crab is currently tracked in both eastern and western subdistricts (divided by the 173° W longitude line); however, the stock is managed as a panmictic unit with a single harvest quota (Bowers et al. 2008). Investigations into population structure have not examined connectivity among northern populations, for which little biological, spatial, and genetic information is available (see, Paul et al. 1997, Merkouris et al. 1998, Bluhm et al. 2009, Rand and Logerwell 2011). Idealized

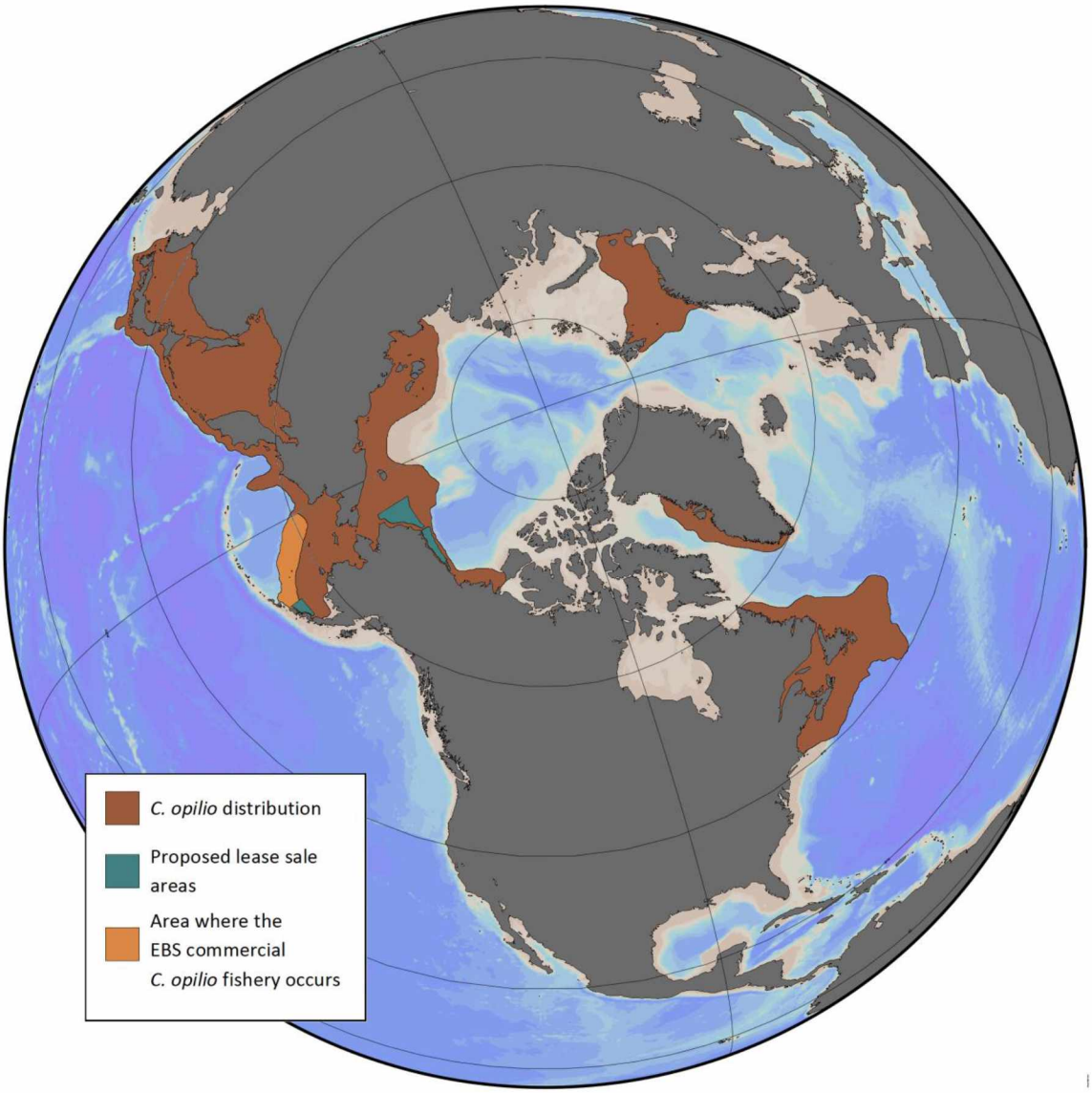

Fig. 1. Known distribution of snow crab (maroon) with oil and gas lease areas (teal) and the Bering Sea commercial fishery (tan) highlighted (based on Rathbun 1925, Atkinson and Wacasey 1989a, Squires 1990, Fütterer 1994, Kuzmin 2000, Burmeister 2002, USDOI-BOEMRE 2010).

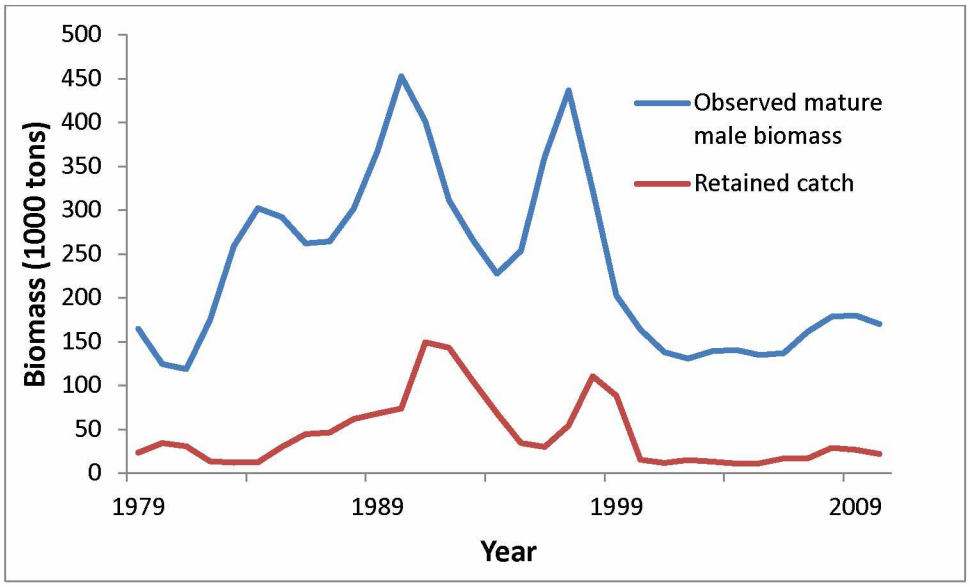

Fig. 2. Observed mature male snow crab biomass and total retained catch, from the Eastern Bering Sea during 1979-2010 (figure produced using data from snow crab stock assessment; NPFMC 2010).

oceanographic flow is assumed to promote northward larval transport from the Bering Sea into the Chukchi and Beaufort Seas, suggesting potential downstream effects of pressures exerted on the southern portions of the population. In addition to commercial fishing pressure, snow crab are subject to a variety of impacts associated with sea-ice retreat and warming trends through direct and indirect pathways such as increased bottom water temperatures and altered predator-prey interactions (Orensanz et al. 2004, Mueter and Litzow 2008, Mueter et al. 2009). Changes in the density distribution of snow crab have been documented over the last four decades, including a substantial northward contraction thought to be related to increases in near-bottom temperatures in the late 1970s and the reduced seasonal ice extent in the Bering Sea (Orensanz et al. 2004). Furthermore, large increases in snow crab biomass have been reported in the Chukchi Sea over the last 30 years, providing additional support for the idea of a northward contraction (Bluhm et al. 2009). Snow crab recruitment in the southern region of the EBS may be impacted by increased abundance of warmer water predators such as Pacific Cod

(*Gadus macrocephalus*) and the predominantly northward flow of currents that disperse larvae (Orensanz et al. 2004, Mueter and Litzow 2008, Parada et al. 2010). Although shifts in temperature and sea ice are thought to be the primary drivers of these changes (Mueter and Litzow 2008), recent work suggests that snow crab density may be playing the largest role in population contraction and expansion, with declines in density resulting in range contractions (Mueter unpub. data). A slight increase in total mature male biomass in all areas, including those in the southern portion of the EBS, was recorded for 2009 and 2010 survey years; however, this trend is not expected to continue based on immature crab abundance (NPFMC 2010). Due to these findings, identifying connections to northern populations has become critical.

Here, through the use of microsatellite techniques, I explore population structure and connectivity on both regional and trans-Arctic scales in Alaskan and NW Atlantic snow crab. While genetic stock structure of snow crab has been investigated previously (see Merkouris et al. 1998), this is the first study to employ sensitive microsatellite techniques, and the first to incorporate individuals from lesser-studied northern portions of the species range. Furthermore, investigations into historical trans-Arctic connectivity of the species may provide insights into past climate trends, migration patterns, and the potential for this species to expand and shift its range.

Study region

The Bering, Chukchi, and Beaufort Seas (Fig. 3) comprise a system of seasonally ice-covered continental shelves, slopes, and basins. In addition to snow crab, the Bering Sea harbors large populations of commercial species such as Pacific cod, walleye pollock (*Theragra chalcogramma*), Pacific halibut (*Hippoglossus stenolepis*), Pacific salmon (*Oncorhynchus* spp.), and red king crab (*Paralithodes camtschaticus*; Springer et al. 1996, Chilton et al. 2011). This ecosystem relies heavily upon the layer of surface water created by melting sea-ice that is relatively fresh and buoyant. Within this warm and

stable lens, high levels of primary production occur, which contribute a significant portion of carbon flux into the ecosystem

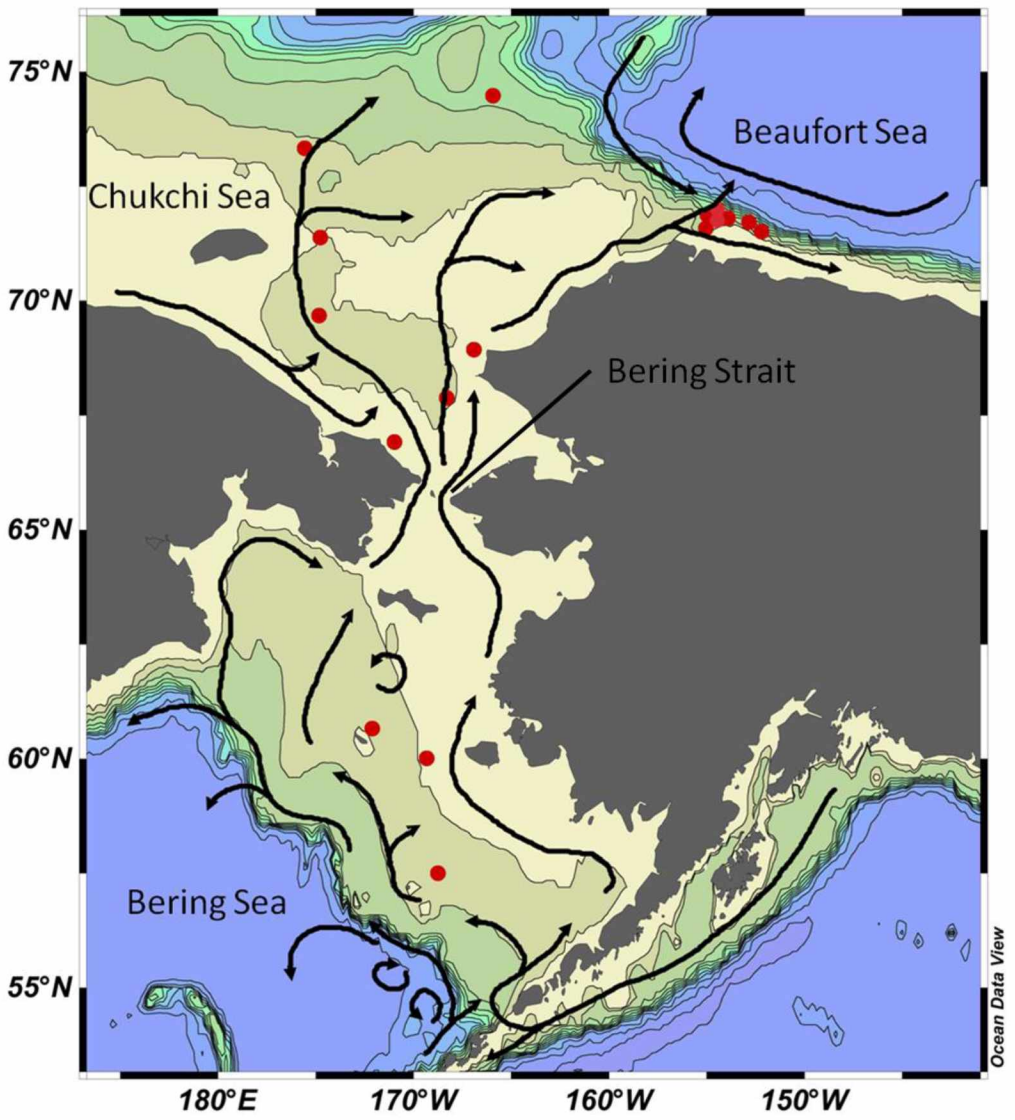

Fig. 3. Idealized oceanographic flow through the study area (black arrows) with sampling stations shown (red dots) (based on Stabeno et al. 2001, Weingartner et al. 2005, Parada et al. 2010).

(Alexander and Niebauer 1981). Primary production in the Chukchi and Beaufort Seas is influenced by similar processes; however, smaller Arctic fishes, primarily cottids, gadids, stichaeids, and pleuronectids, such as the Arctic staghorn sculpin (*Gymnocanthus tricuspis*), polar cod (*Boreogadus saida*), stout eelblenny (*Anisarchus medius*), and Bering flounder (*Hippoglossoides robustus*) are dominant (Norcross et al. 2009, Rand and Logerwell 2011). Furthermore, overall benthic biomass is dominated by invertebrates, including echinoderms such as the notched brittle star (*Ophiura sarsi*), holothurians (*Myriotrochus rinkii*), urchins (*Strongylocentrotus pallidus*), and snow crab (Bluhm et al. 2009, Rand and Logerwell 2011). Chukchi Sea snow crabs, on average, are much smaller [few crabs >65mm carapace width (CW)] than those commonly found in the Bering Sea (adult males >101 mm CW; Paul et al. 1997, Chilton et al. 2011) and the more recently-discovered large individuals of the Beaufort Sea slope (males >101 mm CW; Rand and Logerwell 2011).

The EBS shelf lies between the Alaska Peninsula and the Bering Strait, extending over 600 km from the shore in some areas (Stabeno et al. 2001). This area is typically discussed in terms of three domains bordered by the 50 and 200-m isobaths (Inner Domain 0-50 m, Middle Domain 50-100 m, Outer Domain 100-200 m; Stabeno et al. 2001). Mean flow in the Bering Sea is primarily northward, driven by differences in steric sea level between the Pacific, Arctic, and Atlantic oceans (Stigebrandt 1984). Currents are typically slower over the Middle and Inner Domains (1-5 cm/s) than the Outer Domain (15 cm/s; Schumacher and Stabeno 1998; Reed and Stabeno 1999). Flow through the Bering Strait varies seasonally and can be reversed for periods of time due to wind forcing from the northeast; however, mean flow travels northward through the strait at 10-20 cm/s (Roach et al. 1995, Woodgate et al. 2005). Individual-based models suggest crab larvae and other plankton may be retained locally by microcurrents and eddies that occur northeast of the Pribilof Islands and southwest of St. Matthew Island, or transported long distances from the outer NW Bering Sea into the S Chukchi Sea (approx. 1000 km; Parada et al. 2010).

Air temperatures over the EBS vary on both short and long time scales and are influenced by the strength of the Aleutian Low Pressure System, the El Niño Southern Oscillation, the Pacific Decadal Oscillation, winds generated in the Arctic, and their combined effects on the timing and extent of seasonal ice cover (Stabeno et al. 1999, Stabeno et al. 2001). Annual ice can form as early as November and persist until June, depending on air temperatures and wind speed/direction (Stabeno et al. 2001). The ice is responsible for a large body of cold water that forms over the Middle Domain. Cold water is mixed throughout the water column during the winter. As ice retreats, cold water becomes trapped below a relatively warm and fresh layer of melt water (Stabeno et al. 2001). This cold pool layer can be 40-50 m thick and generally persists throughout the summer, covering most of the Middle Domain (Wyllie-Echeverria and Wooster 1998, Reed and Stabeno 1999, Stabeno et al. 2001). Summer bottom water temperatures across the entire Bering Sea shelf recorded on the 2010 National Marine Fisheries Service (NMFS) trawl survey cruise varied from -1.7 to 6.3°C (NPFMC 2010), while temperatures on the slope and outside of the cold pool tend to be slightly warmer (Grebmeier et al. 2006). The variable extent of the cold pool is known to influence distribution of snow crab and many of their predators (e.g., *T. chalcogramma* and *G. macrocephalus*), which prefer temperatures >2°C (Zheng and Kruse 2006, Mueter and Litzow 2008).

The Chukchi Sea covers a wide continental shelf (~800 km north/south) generally ~50 m in depth that drops off into the Canada Basin relatively quickly in the east and merges with the East Siberian Sea in the west. Bottom temperatures typically remain near freezing year-round, except for a late spring rise to ~ 3°C with the influx of Bering water (Weingartner et al. 2005). Flow is predominantly northward and channeled by the various shoals and valleys in the central a nd northern portions of the sea. Although the velocity of flow through the Bering Strait is relatively fast (10-20 cm/s), flow across the Chukchi shelf typically slows to ¼ of that speed (5 cm/s), due, in part, to wind forcing from the north (Woodgate et al. 2005). After transiting the Chukchi shelf, water reaching the shelf break becomes entrained in an eastward-flowing water mass headed for the Beaufort shelf, or spills into the Canada Basin and travels clockwise in the Beaufort Gyre

(Weingartner et al. 2005). Typical residence time for a parcel of water in the Chukchi Sea varies between 6 and 30 months (Winsor and Chapman 2004). However, flow can be completely reversed to the south due to strong winter winds making these transit times highly variable among years (Aagaard et al. 1985, Winsor and Chapman 2004, Weingartner et al. 2005).

The W Beaufort Sea is bounded by a narrow continental shelf ~50 km wide and <60 m deep. The western portion is defined by Barrow Canyon, a narrow, deep feature responsible for draining a large amount of Chukchi water into the Canada Basin (Weingartner et al. 2005). Flow across the shelf is predominantly eastward but variable; cross-shelf transport is also thought to occur (Garrison and Becker 1976, Pickart 2004). As in the Chukchi Sea, bottom temperatures range between near freezing and ~3°C. Warm Atlantic water (>0°C) is present off the shelf break below the thermocline, with maximum temperatures (<3°C) occurring around 450 m depth (Pickart 2004). Benthic assemblages are similar to those of the Chukchi Sea with echinoderms and crustaceans dominating the biomass; however, the collection of larger sized snow crab (up to 119 mm CW) at deeper stations (306 to 478 m) represented the first record of legal sized crabs caught north of the Bering Strait (Rand and Logerwell 2011). Although few trawls have been conducted in the eastern portions of the Beaufort Sea and high Canadian Arctic, snow crab appear to be absent east of the Mackenzie River Delta (Atkinson and Wacasey 1989b, Burmeister 2002, B. Sainte-Marie, Maurice Lamontagne Institute, Fisheries, and Ocean Canada, Mont-Joli, Quebec, personal communication, 2011).

Snow crab life history review

Snow crab have been observed to form large breeding aggregations ("female mounds") that may work to attract males from long distances (Conan et al. 1996). Males typically deposit enough sperm to fertilize at least two clutches of eggs and can fertilize up to six females per month in a laboratory setting (Watson 1972). Females can store sperm in the spermathaeca, which can be used in the event of a clutch loss between matings, when a

mate cannot be found, or for the avoidance of mating, which can be taxing to the female body (i.e., lost limbs and grasping injuries; Elner and Beninger 1992). Females are capable of mating several times and fertilizing multiple clutches of eggs with sperm stored in the spermathaeca for up to 2 years (Elner and Beninger 1992).

Fertilized eggs are extruded and carried under the female's abdominal flap. The duration of the brooding period can vary, and is typically 1-3 months longer in primiparous females (first-time breeders) which mate 1-3 months earlier than multiparous females in the EBS. Hatching occurs in the spring (March-July) for both primiparous and multiparous females (Orensanz et al. 2004). However, temperature influences whether the brooding period will last one or two years. In a study of Atlantic snow crab, Moriyasu and Lanteigne (1998) concluded that a threshold of degree-days can cause transition between 1- and 2-year cycles. Crabs spending a majority of the time at temperatures between -1 and 1°C (as in the Southern Gulf of St. Lawrence) will typically undergo a 2-year incubation, whereas those that move into warmer waters (1-5°C) will shorten this time period to 1 year (Sainte-Marie and Carriere 1995). The EBS cold pool is typically <2°C; however, the proportion of crabs in either a single or multi-year incubation cycle is not known. Laboratory studies of Bering Sea snow crab show that temperatures experienced within the first 3 months of development are most influential in determining a 1- or 2-year brooding cycle (Webb et al. 2006). The brood period of the Arctic (Chukchi – Beaufort) population is unknown, but a more extensive cold-water presence (Pickart 2004, Weingartner et al. 2005) may support a 2-year incubation period.

Oviposition and hatching typically occur from March to July in the Bering Sea (Somerton 1981a, Zheng et al. 2001). The exact timing of the larval release is suspected to be influenced by environmental conditions such as increased tidal currents and biological cues. Stevens and Haaga (1994) observed Tanner crab releasing their larvae from atop small mounds of sediment, presumably built by the crabs to encourage better dispersal; snow crab may have similar behaviors. According to Starr et al. (1994) the presence of senescent phytoplankton in laboratory and field experiments was found to correlate with

snow crab larval release. The vertical flux of detritus deposited during sea-ice retreat and the associated spring phytoplankton bloom may signal the presence of copepod nauplii, a valuable prey item for crab larvae, in the surface waters.

Snow crab embryos first enter the water column as zoea, a planktonic larval stage typical of crustaceans. At this stage, mobility is limited to vertical swimming, and thus subject to the movements of ocean currents (Mileikovsky 1973). Snow crab have two zoeal stages (zoea I and zoea II) encompassing a single molt. The length of the zoeal stage typically spans three to four months and larvae are found between April and June in the EBS (Incze et al. 1987). However, temperatures during egg incubation can affect morphology (spine lengths) and development time, contributing to spatial variation in length of larval period (Webb et al. 2006). In the EBS, zoeal stages occupy the upper mixed layer where temperatures and food availability are more suitable (Incze et al. 1987). Tanner crab zoea, which co-occur with snow crab larvae in some areas of the Bering Sea, have a diet composed of both zooplankton and phytoplankton, with calanoid copepods being the dominant component (Incze and Paul 1983, Rosenkranz et al. 2001).

Chionoecetes zoeae are likely vulnerable to most pelagic planktivores such as pollock, salmon, herring, and gelatinous zooplankton (Kruse et al. 2007). Moreover, in order to grow, decapod crustaceans must undergo ecdysis, the process through which the exoskeleton is shed and rapid growth ensues in a "soft-shell state" before re-calcification. During the soft-shelled larval stage, or instar, the crab will rapidly swell as a result of water intake. Calcium is then absorbed from seawater in the form of calcite and aragonite to create a hard exoskeleton, beneath which the water can be replaced with actual tissue growth. Crabs are typically more vulnerable to predation during the instar stages, as they lack a hard shell for protection (Brusca and Brusca 2003).

The second molt in the snow crab life cycle marks the entrance into the megalopa phase, where the crab takes on morphology more similar to that of an adult and thus exchanges planktonic life for benthic (Kon 1980, Lovrich et al. 1995). The megalopa stage

encompasses a single molt and is thought to last about 30 days in the Bering Sea (Kruse et al. 2007), during which time the larva will search for suitable benthic habitat and settle. The juvenile stages include the first 7-9 instars, typically encompassing the first four years of life (Sainte-Marie et al. 1995).

In the EBS, juvenile recruitment is the strongest over the Middle Domain, where temperatures are typically <2°C due to the presence of the cold pool (Ernst et al. 2005, Zheng and Kruse 2006). Juvenile snow crab are highly stenothermic, and recruitment is thus strongly influenced by the extent and position of the cold pool (Lovrich et al. 1995, Parada et al. 2010). Field and laboratory observations of Atlantic snow crab show that early juvenile stages (up to instar V) are the most stenothermic, preferring temperatures <1.5°C (Dionne et al. 2003).

Preferred juvenile habitat consists of mud or gravel bottoms at depths between 50-100 m (Zheng et al. 2001). Laboratory trials show that temperature is more influential in habitat selection than substrate type (Dionne et al. 2003). Nonetheless, megalopae and instars I-V have limited mobility and typically bury into the sediment, remaining highly sedentary (Kon 1980, Lovrich et al. 1995). Young-of-the-year crabs remain buried in the sediment with only eyes and rostrum exposed to avoid predation pressure (Rosenkranz et al. 2001), which is exerted by a variety of fish and invertebrates, including adult snow crab (Livingston 1989, Lovrich and Sainte-Marie 1997).

During the juvenile phase, crabs may molt numerous times within a single year until the terminal molt to maturity occurs (Somerton 1981a). Juvenile and adult snow crab exhibit opportunistic feeding behavior and typically consume items such as crustaceans, echinoderms, polychaetes, mollusks, detritus, fish, and plants (Tarvirdieva 1976, Lovrich and Sainte-Marie 1997). Snow crab begin cannibalizing members of their own species around 32 mm CW, so long as they are at least twice the size of the prey. Furthermore, occurrence of cannibalism is shown to increase with population density, particularly in

areas of steep topography, which can allow for greater overlap of crabs of various size classes, which often inhabit different depth (Lovrich and Sainte-Marie 1997).

Adolescence (one or more instars/years for males) is marked by development of primary sexual characteristics and movement within the EBS towards the outer Middle Domain (Ernst et al. 2005). The presence of spermatophores in males and ovaries in females indicate primary sexual maturity. In the NW Atlantic, males develop primary sexual characteristics at 31-40 mm CW, while those collected from the Chukchi Sea do so at 25-29 mm CW (Paul et al. 1997, Sainte-Marie et al. 1997). Although this information is not documented for the Bering Sea, maturity is likely reached at a larger size than that of Chukchi crabs due to increased growth associated with warmer temperatures experienced at lower latitudes (Somerton 1981b, Paul et al. 1997, Orensanz et al. 2004).

Development of secondary sexual characteristics occurs during the terminal molt to maturity. Morphometric maturity (development of secondary sexual characteristics) is marked by a disproportionately large increase in the size of the dominant chelae (males) and abdominal flap (females; Somerton 1981a, Otto 1998, Burmeister and Sainte-Marie 2010). Size at maturity decreases with latitude (females: 70 mm CW at 55° N latitude to 40 mm CW at 63° N latitude) (Somerton 1981a, Somerton 1981b). This pattern is likely due to positive correlation between temperature and growth, which has also been observed in NW Atlantic stocks (Burmeister and Sainte-Marie 2010). Sainte-Marie et al. (2005) showed that average size in the NW Atlantic increases from 52 mm in Baie Sainte-Marguerite to 71 mm in the Saguenay Fjord over a gradient of 2-3°C.

The terminal molt in the EBS occurs during the winter and early spring (Feb-May) in males, and during the winter only (Feb-March) in females (Ernst et al. 2005). Terminally molted crabs are found in the highest abundances in deeper waters along continental shelf break-slope areas (100-200 m) in the EBS (Ernst et al. 2005). Age-at-maturity ranges from 4.5-7.5 years post-settlement in the Gulf of Saint Lawrence, and 7-8 years in Bonne Bay, Newfoundland (Alumno-Bruscia and Sainte-Marie 1998, Comeau et al. 1998). EBS

crab mature 5-10 years (males) and 3-7 years (females) after settlement (Kruse et al. 2007). Males spend a longer period of time in the adolescent stage, during which time the size increase between molts begins to differ between the sexes as males grow faster than females (Sainte-Marie and Carriere 1995). Time between terminal molt and death is estimated at up to 7 years in the EBS, for a total life span of 14 years in females and 17 in males (Ernst et al. 2005, Shirley and Bluhm 2005).

Having reached sexual maturity, males are able to attempt mating when in the hard shell state (Hartnoll 1969). Relative mating success of morphometrically immature (MI) males in the wild, however, is a topic of some debate (see Conan and Comeau 1986, Elner and Beninger 1992, Sainte-Marie et al. 1997, Sainte-Marie et al. 2008). Laboratory studies revealed that when placed in a competitive situation, the largest morphometrically mature (MM) crabs were the most successful in inseminating primiparous females, followed by smaller MM crabs, large MI crabs, and small MI crabs (Sainte-Marie et al. 1997). Additionally, multiparous females only successfully mated with MM males (Sainte-Marie et al. 2008). However, in a noncompetitive context, MI males were capable of passing amounts of sperm comparable in both volume and potency to that of similarly sized MM males to female crabs (Moriyasu and Conan 1988, Sainte-Marie and Lovrich 1994).

In the wild, there appears to be spatial and temporal separation of adolescent and adult mating behavior, with primiparous females typically mating shallower and earlier in the year than multiparous females (Yamasaki and Kuwahara 1992, Lovrich et al. 1995, Ernst et al. 2005). Primiparous mating most likely occurs in the winter in the EBS, 1-3 months prior to multiparous mating (March-July) over the outermost portions of the Middle Domain (100 m) (Somerton 1981a, Sainte-Marie and Hazel 1992, Ernst et al. 2005). Although Conan et al. (1989), in their research concerning the bipartite mating hypothesis in Tanner crabs, suggests that primiparous females mate predominantly with adolescent males, this view has been challenged by more recent field observations supporting an onshore migration of adult males for the primiparous mating season in N Atlantic populations (Lovrich et al. 1995, Sainte-Marie et al. 2008).

Migration and spatial distribution

Snow crab have been documented at depths ranging from 4 to 520 m in the Pacific, with large males found at depths up to 1400 m in the NW Atlantic (Yosho and Hiyashi 1994, Lovrich et al. 1995, Dawe and Colbourne 2002). Newly settled juveniles occur in the largest concentrations at 50-100 m in the Bering Sea (Middle Domain), and in the NW Atlantic (see discussion in Comeau et al. 1998, Ernst et al. 2005). Temperature is thought to strongly affect habitat choice of juvenile crabs, as they are the most stenothermic at this stage (Dionne et al. 2003). Thermal, substrate, and dissolved oxygen tolerances increase with age such that population density and mating opportunities become more important in governing distribution of adolescent and adult stages (Comeau et al. 1998, Dionne et al. 2003).

Newly matured females in the EBS undergo an ontogenetic migration from the Middle Domain towards the Outer Domain (Ernst et al. 2005). In addition to moving deeper, the direction of movement (S/SW) is generally "upstream" with respect to local currents that influence larval dispersal. Adult females in the central Bering Shelf migrate over distances averaging 84.6 km (Ernst et al. 2005). Although male migration patterns are not as well understood in the EBS, size-frequency data based on shell condition index suggest that males migrate to deeper waters following the terminal molt (Otto 1998). This pattern has been documented in NW Atlantic populations; however, MM males are known to migrate to shallower waters for mating with primiparous females—a phenomenon that has not yet been documented in the EBS due to trawl survey timing and seasonal ice cover (Sainte-Marie and Hazel 1992, Lovrich et al. 1995, Otto 1998). This continued movement of adult males, in contrast to the sedentary nature of mature females, is likely to promote sex-biased gene flow within a given region.

Movement patterns of crabs within the Chukchi and Beaufort Seas are not known; however, mature females have been found throughout the Chukchi shelf (<50 m), interspersed among new-shell crabs (Paul et al. 1997, S. Hardy, University of Alaska

Fairbanks, Institute of Marine Science, personal communication, 2011). Migrations to deeper water may be evidenced by the discovery of large males (up to 119 mm CW) and females (up to 78 mm CW) in waters ranging from 306–478 m in the Beaufort Sea (Rand and Logerwell 2011). Determining whether these crabs comprise a separate genetic stock, are significantly older, or are simply larger due to exposure to warmer temperatures, is of interest given that crabs of this size have not been found elsewhere north of Bering Strait (Paul et al. 1997, Bluhm et al. 2009).

Population connectivity and implications for fishery management

High levels of connectivity are often found to exist in marine organisms with long planktonic phases occurring in systems lacking obvious barriers to dispersal (Palumbi 1992, Tepolt et al. 2009); however, recent studies show this is not always the case (see Taylor and Hellberg 2003, Becker et al. 2007). Management of separate genetic stocks has been recommended for Dungeness (*Metacarcinus magister*) and NW Atlantic snow crab (*C. opilio*) populations based on microsatellite studies (Bunch and Highsmith 1998, Beacham et al. 2008, Puebla et al. 2008) and investigations into king crab that reveal structuring on small scales are ongoing (Vulstek unpub. data). Similarly, size-frequency distribution and genetic evidence have led to the ongoing management of Tanner crab in two separate subdistricts in the EBS (Somerton 1981a, Zheng and Pengilly 2011). In Atlantic cod (*Gadus morhua*), genetic evidence has played a large role in the designation of separate management units (Beacham et al. 2002, Hauser and Carvalho 2008). Given that Alaskan snow crab occur on similar spatial scales and in comparable oceanographic settings as these species, there is potential for genetic structure. Previous investigations into snow crab show little population structure among three sites within the EBS; however, allozyme techniques were used and northern populations were not analyzed (Merkouris et al. 1998).

Oceanographic flow is relatively unbroken in the Alaskan study area, but local retention of snow crab larvae within eddies may occur (see Lee et al. 1994, Parada et al. 2010) which could influence genetic structure. Due to a primarily northern oceanographic flow,

connectivity and the relative contribution of larvae from Bering Sea stocks to recruitment in Arctic populations must be considered so that more informed decisions can be made regarding the future management of northern stocks. Although snow-crab fisheries do not currently exist in the Chukchi and Beaufort Seas, warming trends may make these areas increasingly available to harvest activity, as well as resource exploration and extraction. Understanding the connectivity in these areas is important and genetic analysis may be able to reveal the origins of newly discovered legal sized crabs in the Beaufort Sea. Validation of the current EBS snow crab management approach is also necessary, particularly when considering recent population declines and range shifts. Population dynamics of snow crab are tracked in the eastern and western EBS subdistricts, but management decisions are made based on the health of the population as a whole.

Historical connectivity between Atlantic and Pacific snow crab populations has not been explored and the absence of snow crab from the Canadian Arctic remains unexplained. Previous work suggests low divergence between snow crab from these two regions; however, connectivity through larval dispersal is highly unlikely given the distance separating these regions (>3,000 km; Merkouris et al. 1998). Further investigations into levels of divergence and historical connectivity may provide valuable insights into the timing and nature of the species' trans-Arctic range expansion.

Therefore, I combine knowledge of life history information with genetic analysis to explore snow crab population structure throughout their Alaskan and NW Atlantic distribution. More specifically, I test the hypothesis that snow crab in the Bering, Chukchi and Beaufort Seas form a panmictic population that experiences sufficient gene flow to prevent population subdivision throughout the region. Furthermore, to gain insight into the history of the dispersal of the species, I test the hypothesis that significant genetic differentiation occurs between Alaskan and NW Atlantic snow crab, which currently inhabit distinct, non-overlapping geographic regions.

Materials and Methods

Sample collection

Field sampling was conducted in the Beaufort, Chukchi, and Bering Seas between 2008 and 2010 (Fig. 4). Collection information for all samples is summarized in Table 1. Beaufort Sea samples (*n =145*) were collected in August 2008 during a US Minerals Management Service expedition aboard the F/V *Ocean Explorer* using an 83-112 eastern otter trawl (for cruise details see Rand and Logerwell 2011). Subsampling was conducted at stations where snow crab were highly abundant and samples were frozen whole aboard the vessel at -20°C. and transferred to -80°C in the home laboratory. Samples from six stations (2, 4, 22, 23, 24 and 26; Fig. 4) were combined due to low sample numbers, proximity to each other and similarity in size of individuals. Sample sizes large enough for genetic analysis, based on polymorphism of loci used, were collected at stations 7 and 8. Furthermore, substantially larger individuals were present at these sites (≥86.2 ±15.2 mm, compared to 34.6±15.2 mm avg. CW), suggesting they may represent a separate stock. Overall sampling effort for the cruise targeted water masses associated with three depth strata (20-50 m, 51-100 m and 101-500 m) that may influence demersal and benthic fish distribution. Snow crab samples were collected opportunistically, so sample sizes varied.

Chukchi Sea samples (*n = 268*) were collected in September 2009 during the Russian-American Long-term Census of the Arctic (RUSALCA) cruise aboard the R/V *Professor Khromov*, using otter and plumb-staff beam trawls. As many as 50 females were collected from each of seven stations to encompass a broad area (Fig. 4, Table 1). Both male (*n = 17*) and female (*n = 7*) crabs were analyzed from the N Chukchi Shelf site (NC). Fewer crabs were obtained at this site, yet it represents an important data point as it is the farthest-north collection location. The majority of Chukchi crabs collected were immature (92.4% females only) and assumed to not have moved great distances since settlement (Lovrich et al. 1995, Ernst et al. 2005).

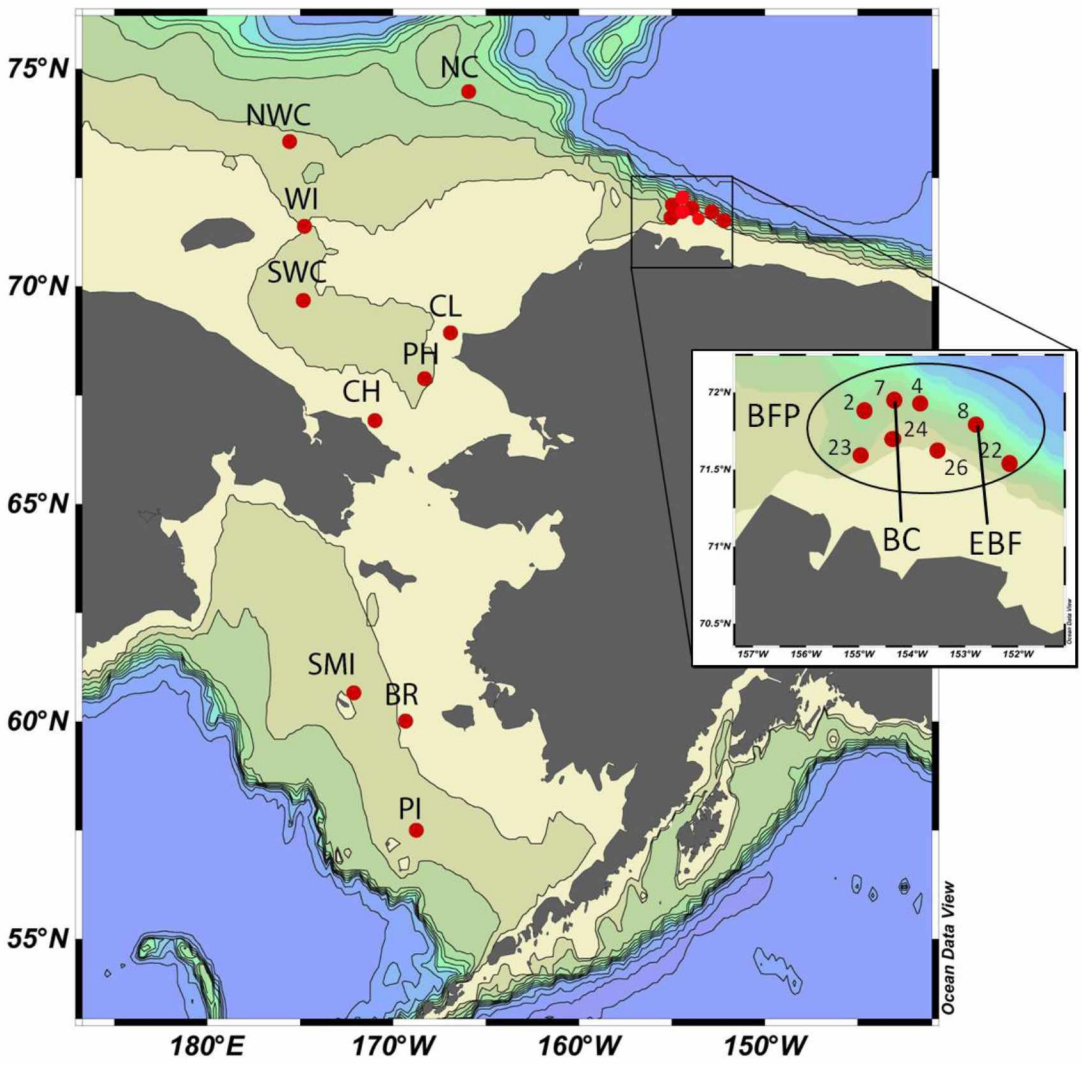

Fig. 4. Map showing sample locations (red dots). Station BFP (inset) in the Beaufort Sea represents samples pooled from sites 2, 4, 22, 23, 24 & 26 (site numbers correspond to Rand and Logerwell 2011).

Table 1. Summary of trawl station and sample collection information for Alaska region data. Station abbreviations correspond to those in Fig. 4; (*N*) number of males (*m*) and females (*f*) analyzed from each station; depth in meters at each station; latitude and longitude at each station; (Avg. CW) mean carapace widths of individuals collected at each sampling site ± standard deviation in millimeters.

Site Name	Abbreviation	*N*	Depth (m)	Lat (N): Long (W)	Avg. CW (mm)
Pribilof Islands	PI	77*f*, 23*m*	71	57.50 : -168.75	50.5±6.1
Bering Sea	BR	50*f*	47	60.01 : -169.33	*
Saint Matthew Island	SMI	50*f*	61	60.66 : -172.12	43.9±4.0
Chukotka Coast	CH	50*f*	53	66.56 : -170.59	33.5±5.7
Point Hope	PH	*29f*	57	67.88 : -168.31	46.3±5.1
Cape Lisburne	CL	39*f*	47	68.57 : -166.55	35.4±4.5
SW Chukchi Shelf	SWC	50*f*	54	69.41 : -174.51	44.1±5.9
Wrangel Island	WI	26*f*	86	71.24 : -174.47	45.5±5.6
NW Chukchi Shelf	NWC	50*f*	146	73.21 : -175.34	35.6±4.4
N Chukchi Shelf	NC	7*f* 17*m*	350	74.30 : -165.57	36.1±15.3
E Beaufort Slope	EBF (*station: 8*)	4*f* 36*m*	320	71.72 : -152.84	82.1±14.8
Barrow Canyon	BC (*station: 7*)	8*f* 65*m*	334	71.98 : -154.41	88.5 ± 15.0
	BFP (*station:2)*	4*m*	478	71.89 : -154.95	25.4±3.1
	BFP (*station: 4)*	1*f* 4*m*	356	71.90 : -153.91	20.5±3.4
	BFP (*station: 22)*	5*m*	182	71.51 : -152.20	34.6±14.4
Beaufort Sea Pooled	BFP (*station: 23)*	3*f*, 3*m*	45	71.58 : -155.05	37.1±11.5
	BFP (*station: 24)*	2*f*, 4*m*	49	71.68 : -154.48	30.4±6.8
	BFP (*station: 26)*	3*f*, 3*m*	53	71.55 : -153.48	59.5±6.1
	BFP (*all stations*)	9f, 23m			34.6±15.2

*Average CW is not available for this station; however, all females collected within the Bering Sea were between 30-65mm CW and considered to be pre-pubescent/immature.

Bering Sea samples (*n = 200*) were collected in July 2010 aboard the National Marine Fisheries Service (NMFS) annual trawl survey cruises (for cruise report see Chilton et al. 2011). Sampling occured on a 20-nm grid, and was conducted aboard the F/V *Aldebaran* and the F/V *Alaska Knight* using 83-112 eastern otter trawls. All samples for genetic analysis were collected aboard the F/V *Alaska Knight*, with the exception of 50 samples from the Pribilof Island station (PI) that were collected aboard the F/V *Aldebaran* within the same month (Fig. 4, Table 1). Three sampling sites were chosen in an effort to encompass the Eastern Bering Sea distribution of adolescent crabs, which are believed not to have made significant ontogenetic migrations at this stage. Pre-pubescent females (or those one molt prior to maturity) were targeted at each of three sites (*n = 50-100* individuals per site) in order to be consistent with Chukchi sampling and to obtain a snapshot of the female *only* population in the Bering Sea, about which more life-history information is known (Ernst et al. 2005). A 2.5-cm section of the 4th walking leg was sampled from each live crab on board ship, and preserved in 95% ethanol.

DNA extraction and microsatellite analysis

Genomic DNA was extracted from tissues using Omega Bio-Tek E.Z.N.A.® and Qiagen DNeasy® extraction kits. Seven published microsatellite loci were selected and successfully amplified for this analysis: *Cop2, Cop3, Cop4, Cop3-4II, Cop24-3* and& *Cop11* (Puebla et al. 2003) and *EC0106* (An et al. 2007). Attempts to amplify five additional loci (*Cop4-1* and *Cop77*; Puebla et al. 2003 and *KC030*, *KC0181* and *KC0235*; An et al. 2007) were either unsuccessful or yielded unusable amplifications (e.g., irregular stuttering).

A total volume of 10 µl was used in polymerase chain reaction (PCR) mixes and consisted of 1 µl milli-Q water, 1 µl 10x forward and reverse primer (diluted with TE buffer), 5 µl Qiagen hot start *Taq* polymerase multiplex kit (2x; containing a final concentration of 3 mM $MgCl_2$), and 3 µl template DNA. PCR conditions consisted of a 30 minute denaturation at 94°C, followed by 40 cycles of 30 seconds denaturing at 96°C,

50 seconds annealing at 55°C, and 1 minute of extension at 72°C with a final extension time of 20 minutes at 72°C. Three PCR multiplexes consisting of 2 loci each (*Cop113* and *Cop3-4II*, *Cop2* and *ECO106*, *Cop3* and *Cop4*) were used; however, *Cop24-3* was run independently due to interference when paired with any other locus. Final PCR product was submitted to the Yale DNA Facility (*http://dna-analysis.research.yale.edu//*) for capillary electrophoresis on a 3730 *x*/ 96 Genetic Analyzer with LIZ500 size standard. All samples were amplified, analyzed, and scored independently a minimum of two times to ensure accurate genotyping with a range of 0-8.5% missing data per locus.

Descriptive statistics and population differentiation

Allele scoring was conducted using GeneMapper® software (version 3.7. Applied Biosystems). Tests for departures from Hardy-Weinberg equilibrium (HWE) and the presence of null alleles and stuttering were calculated by comparing sets of observed and randomized alleles using a cumulative binomial distribution (Weir 1996), and tested for significance using Fisher's combined probability test, as implemented in the program MICRO-CHECKER (version 2.2.3; Van Oosterhout et al. 2004). All loci were tested for linkage disequilibrium (LD), which is a test for non-random association of alleles at different loci (e.g. physical linkage or selection). LD tests were carried out using a Markov chain method to provide unbiased *p*-values for results of a contingency table analysis performed in GENEPOP (version 4.0; Rousset 2008) with 10,000 batches and 20,000 iterations per batch. Evidence of LD was detected at one station in the Beaufort Sea (EBF; see below), and additional tests were performed to determine the cause of significant tests for LD. The *M*-ratio (Garza and Williamson 2001) was used to detect historical bottlenecks. This metric is calculated as the number of alleles in a given sample divided by the total number of possible allelic states. The program BOTTLENECK (version 1.2.02; Piry et al. 1999) was used to test for a heterozygote excess, as would be expected after a bottleneck, using a Wilcoxon signed-rank test with 10,000 iterations in the EBF sample site only. Two separate tests for relatedness among individuals at EBF (cf.

Queller and Goodnight 1989, Ritland 1996) were performed using GenAlEx (version 6.1; Peakall and Smouse 2006).

To test the hypothesis of panmixia across the study region, a Bayesian clustering approach, implemented in the program STRUCTURE (version 2.3.1; Pritchard et al. 2000), was used to assign individuals to populations (clusters) based on their genotypes. All possible numbers of clusters (K) from 1 (panmixia) to 13 (distinct population at each sampling site) were tested using the admixture and correlated allele-frequency models. For each value of K, a total of five runs were performed with 500,000 Markov Chain Monte Carlo (MCMC) repetitions following a 500,000 repetition burn-in period, and the most likely number of clusters (i.e., populations) was determined based on the *ad hoc* likelihood measures $L(K)$ (Pritchard et al. 2000) and ΔK (Evanno et al. 2005).

In addition to Bayesian analysis of population differentiation, global and pairwise F-statistics, including the F-statistic analogues G_{ST}, G_{IS}, (Nei 1973), as well as expected heterozygosity (H_e) were calculated using the R statistical-software package DEMEtics (Jueterbock et al. 2010) with 1000 bootstrap replicates. Because G_{ST} can perform poorly in high-diversity populations (Gerlach et al. 2010) such as those examined here, Jost's (2008) measure of true differentiation (D) was also calculated in DEMEtics with 1000 bootstrap replicates. Calculations for observed heterozygosity (H_o) were performed in GENODIVE (version 2.0; Meirmans and Van Tienderen 2004). Allelic richness, rarefied for the smallest sample size present (n = 24), was calculated using HP-RARE software (Kalinowski 2005) and a Wilcoxon signed-rank test was carried out in the statistical software package JMP (SAS institute, Cary, NC, USA) to test for significance between sampling sites. Pairwise-comparisons of allele frequencies among all sample sites and regions were performed using Fisher's exact test as implemented in the software GENEPOP (Raymond and Rousset 1995), with 10,000 batches and 10,000 iterations.

The application of Jost's D (2008), likely the most sensitive measure employed here, is appropriate, particularly as a supplement to Nei's (1973) G_{ST}. G_{ST} is strongly based on

heterozygosity and mathematically "bounded" by the overall heterozygosity (H_S) within the population (i.e., when H_S is large, G_{ST} cannot reach 1; Nei 1973, Jost 2008). Hedrick (2005) realized this weakness and put forth a new measure (G'_{ST}), which is standardized to overall heterozygosity. However, these two statistics more accurately measure migration rate, which is only a single cause of population differentiation among others (i.e., random sampling of genes at mating, bottlenecks). Jost's D accounts for effective allele frequencies and provides an arguably more ecologically relevant and conservative measures of differentiation (Jost 2009). Due to the fact that a great deal of debate exists around this topic (see Jost 2008, 2009, Ryman and Leimar 2009, Meirmans and Herdrick 2011) and for comparability with other studies, I have employed both measures here.

Meta-population structure and historical analysis

To examine population structure over larger geographic scales, genotype data for five of the microsatellite loci used here (*Cop2, Cop4, Cop3-4ii, Cop24-3 and Cop113*) were obtained from a similar study conducted in the NW Atlantic (Puebla et al. 2008). Because each study used different electrophoresis machines for microsatellite fragment analysis, results needed to be calibrated to account for the slight differences in fragment size that can be generated by different equipment. A subset of 60 individuals from the present study were independently DNA- extracted and analyzed at these five loci by the authors of the NW Atlantic study (J.-M. Sèvingy. Dept. of Fisheries and Oceans, Canada). The average differences between the raw allele scores generated by each lab, as well as scatter plots of all raw allele sizes, were used to correct the Puebla et al. (2008) dataset. Populations identified in Puebla et al. (2008) were then tested for genetic differentiation from Alaskan region populations identified in the present study based on values of G_{ST} and D, and on Bayesian analysis using STRUCTURE (testing K = 1-10 with similar parameters) as described above. An Unweighted Pair Group Method with Arithmetic Mean (UPGMA) tree was constructed using Jost's D values in the program MEGA 5 (Tamura et al. 2011) to visualize genetic distances between regions.

To investigate historical trans-ocean connectivity, coalescent-based Approximate Bayesian Computing methods, employed in the program DIY ABC V.0.7.3 (Cornuet et al. 2008), were used to simulate and evaluate three possible scenarios of historical gene flow/expansion of snow crab populations into the Atlantic Ocean. DIY ABC, designed specifically for microsatellite data, can generate a large number of simulated datasets, of which the posterior distributions of the parameters can then be compared to observed data. Through this process, multiple scenarios can be compared and ranked in terms of likelihood. The approximate timing of warmer ice-free periods in the Canadian Arctic Archipelago (3-5 ka, 8.5-10.5 ka, and 127-130 ka; Dyke et al. 1996, Miller et al. 2010, Polyak et al. 2010) was used to create dispersal scenarios based on an average generation time for snow crab of 6 years (Conan et al. 1989, Alumno-Bruscia and Sainte-Marie 1998, Kruse et al. 2007). Thus, generations since last gene flow for scenarios 1, 2 and 3 ranged from 500-833, 1417-1750 and 21,167-21,667, respectively. A wide range for effective population size (N_e = 1,000-100,000) was used in the scenarios because historical population sizes are unknown. Current mature crab estimates for the EBS are well into the 100s of millions (NPFMC 2010), suggesting that a large N_e of all snow crab at the time of expansion would be realistic. The Generalized Stepwise Mutation model was implemented with default values (Fu and Chakraborty 1998, Estoup et al. 2002) and 500,000 data sets were computed for each scenario.

Results

Descriptive statistics and population differentiation

The seven microsatellite markers used in this study were found to be highly polymorphic with alleles per locus ranging from 12 (*Cop4*) to 41 (*ECO106*; mean = 24.6 ±8.8; Table 2). Rarefied allelic richness (based on the smallest sample size $n = 24$) ranged from 11.35-14.41 (mean = 13.42 ± 0.77; Table 3). Allelic richness did not vary significantly at any two sampling sites (Wilcoxon signed-rank test, data not shown, P = 0.12). Overall observed heterozygosities (H_O) at each locus ranged from 0.228 (*Cop4*) to 0.908 (*Cop24-*

3; mean = 0.773 ±0.244; Table 2). Observed heterozygosity averaged across all loci for each sampling site ranged from 0.721 (PH) to 0.815 (NC; mean = 0.773 ±0.026; Table 3).

Table 2. Alaska region results for number of alleles; size range (base pairs); (H_O) observed heterozygosity; (H_S) gene diversity; (G_{IS}) the measure of individual diversity relative to its subpopulation (in this case sampling site); (G_{ST}) the measure of subpopulation diversity relative to the total; (D) Jost's (2008) measure of differentiation; ± standard deviation.

Locus	Alleles	Size Range (bp)	H_O	H_S	G_{IS}	G_{ST}	D
Cop2	24	291-341	0.835	0.838	0.003	0.000	0.000
Cop3	21	210-318	0.791	0.861	0.081	0.001	0.005
Cop4	12	211-259	0.228	0.267	0.145	0.000	0.000
Cop3-4II	22	119-209	0.865	0.911	0.050	0.002	0.016
Cop24-3	29	145-253	0.908	0.925	0.019	0.003	0.032
Cop113	23	114-166	0.885	0.892	0.007	0.000	0.000
ECO106	41	187-271	0.898	0.959	0.064	0.003	0.080
Mean/Global	24.6 ±8.8	-	0.773 ±0.244	0.807 ±0.242	0.043	0.001	0.004

Significant departures from Hardy-Weinberg equilibrium (HWE) were found in 14 out of 91 possible population-locus pairings (15.4%; Table 3). It is likely that these departures are due to random error associated with genotyping and null alleles, as opposed to actualpopulation dynamics. All significant tests were due to heterozygote deficits and the possible presence of null alleles; however, no more than three significant tests occurred at any site and no more than five were observed for any locus (Table 3). The highest frequencies of HWE departure at a single locus occurred at *Cop3-4II* and *ECO106* (4 and 5, respectively). Although MICRO-CHECKER did not detect evidence for error due to stuttering, these loci produced stutter patterns that may have contributed to a tendency to

miss heterozygotes when being scored due to their wide stutter arrays. In checking for HWE departures due to stuttering, the program MICRO-CHECKER detects significant absences of heterozygotes separated by a single repeat unit, as would be likely to occur if a short stutter band obscured these peaks. These loci, however, often amplify with wide stutter arrays, which could conceal heterozygotes more than one repeat unit away from each other, making it more likely to incorrectly score as a homozygote. A standardized

Table 3. Summary of descriptive statistics at each station for Alaska region data. (*A*) allelic richness over all loci and rarefied to the smallest sample size; (H_O) observed heterozygosity; ± standard deviation; significant departures from Hardy-Weinberg equilibrium (X), based on comparisons of observed and randomized allele frequencies using a cumulative binomial distribution implemented in MICRO-CHECKER.

Sample site	*A*	H_o	*Cop 2*	*Cop 3*	*Cop 4*	*Cop 3-4II*	*Cop 24-3*	*Cop 113*	*ECO 106*
Pribilof Islands (PI)	13.9	0.762		X					X
Bering Sea west of Nunivat Island (BR)	13.9	0.790							
Sainte Mathews Island (SMI)	13.5	0.736		X		X			X
North of Chukotka (CH)	13.6	0.757				X			
Southwest of Point Hope (PH)	13.7	0.721			X	X			
Northwest of Cape Lisburne (CL)	14.0	0.765							X
Southwest Chukchi Sea (SWC)	13.7	0.786				X			
Wrangel Island (WI)	14.4	0.793							
Northwest Chukchi Sea (NWC)	13.4	0.793		X					
Northern Chukchi Sea (NC)	13.5	0.815							
Eastern Beaufort Slope (EBF)	11.4	0.779			X				
Barrow Canyon (BC)	13.2	0.776							X
Beaufort Sea Pooled (BFP)	12.5	0.772							X
Mean	13.42 ±8.8	0.773± 0.026							

*All significant departures from HWE were due to heterozygote defecits.

method of scoring based on peak morphology was implemented, and stutter arrays that were atypical were often re-amplified a number of times, or omitted as missing data.

Tests for linkage disequilibrium (LD) revealed 15 significant results out of 273 tests at each locus combination per site (significance level 0.05/13 = 0.0038). All 15 of the significant results occurred at the Eastern Beaufort Slope (EBF) site, suggesting a site-specific phenomenon rather than a population-wide problem with a particular locus. Significant LD can indicate a population bottleneck, sampling of closely related individuals, or recent immigration. Genotyping error was ruled out by blind scoring procedures, in which individuals were scored prior to grouping within sampling sites for analysis. Tests for heterozygote excess, as would be expected after a bottleneck, were performed in the program BOTTLENECK and were not significant (Wilcoxon one-tailed test p = 0.148, data not shown). BOTTLENECK, however, has been found to poorly identify known bottlenecks in some cases (Hundertmark and Van Daele 2010). Therefore, the *M*-ratio was calculated for the population in question, as it has been shown to more accurately detect bottlenecks, especially older events (Garza and Williamson 2001, Spear et al. 2006). However, using the critical value (0.680) from Garza and Williamson (2001), the EBF population was not found to have significant evidence of a bottleneck (0.732).

Relatedness (calculated with both the methods of Queller and Goodnight 1989 and Ritland 1996) ranges on a scale of -1 to 1, with larger positive values indicating higher than expected relatedness. Both measures showed values near zero, indicating no significant relatedness (-0.013 and -0.027, respectively, data not shown) among sampled individuals in the EBF population. Furthermore, the values for both relatedness tests were not significantly different from those of all other populations (Wilcoxon signed-rank test; $p = 0.457$, data not shown). Therefore, admixture with individuals from an unsampled population appears to be the most likely cause of this result.

Estimates of the posterior probability measure *L(K)* indicated the most likely number of clusters (i.e., populations) to be 1 (Fig. 5). The highest value for the second-order rate of change between values of *K* (*ΔK*) was 3 (Fig. 6). Although *L(K)* has been shown to inaccurately estimate the true value of *K* in some cases (Pritchard et al. 2000, Evanno et al. 2005), *ΔK* can only be applied to values larger than 1 and therefore is not capable of assessing *K* = 1. Furthermore, the decrease in the mean of estimated ln probability between *K* = 1 and *K* = 2 is much larger than that between *K* = 3 and *K* = 4 (Fig. 5). Therefore, the magnitude of *ΔK* between *K* = 3 and *K* = 4 would likely be less than between *K* = 1 and *K* = 2, if such a measure could be calculated. Therefore, I interpret *K* = 1 as the best estimate. The graphical representation of individual clustering at *K* = 3

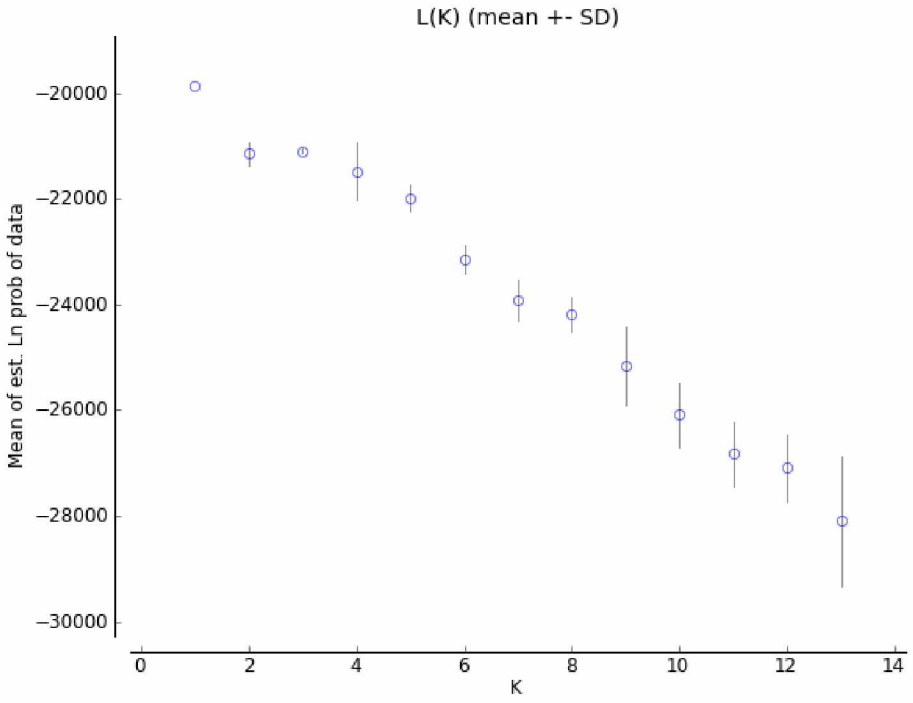

Fig. 5. Mean of estimated ln-likelihood probabilities for all possible values of *K* (clusters) from 1 to 13. Probabilities were estimated using a Bayesian analysis method implemented in the program STRUCTURE and plotted using STRUCTURE Harvester.

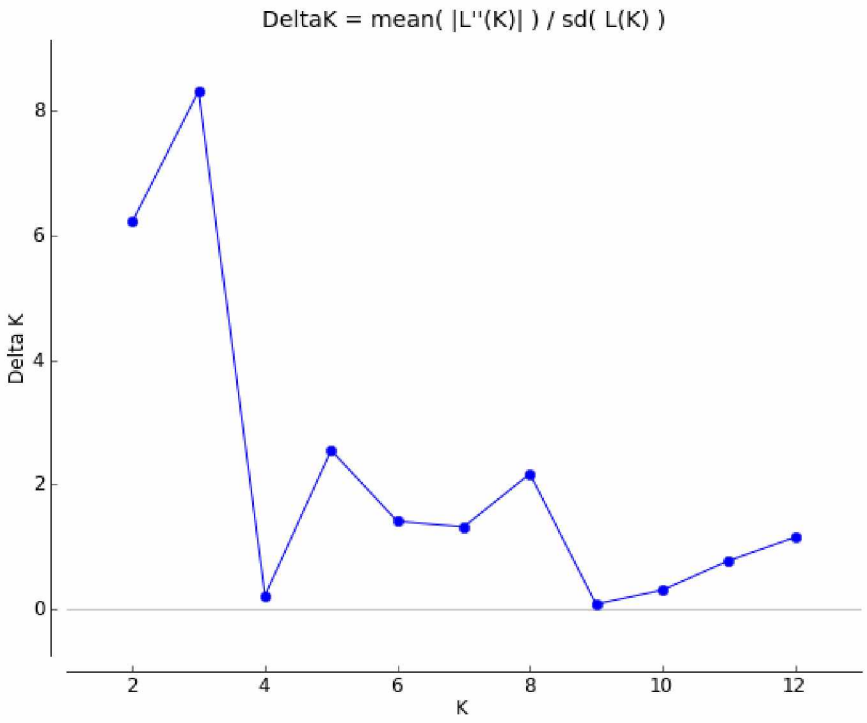

Fig. 6. Second-order rate of change (ΔK) for cluster values of 2-13. Data were generated using a Bayesian analysis method implemented in the program STRUCTURE and plotted using STRUCTURE Harvester.

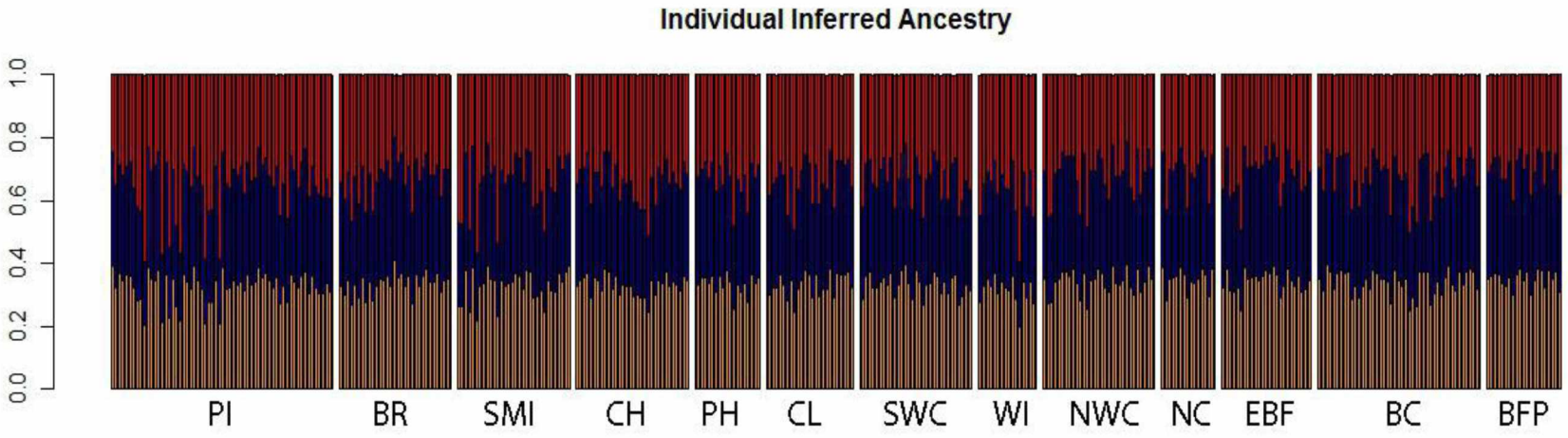

Fig. 7. Graphical representation of clustering from STRUCTURE for Alaskan region analysis. Each vertical line represents the probability that an individual's genotype corresponds to each cluster ($K = 3$).

(Fig. 7; vertical lines represent individuals and the proportion of their genotype that is assigned to each cluster indicated by color), allele frequency comparisons, and *F*-statistics further support the conclusion of $K = 1$ in this analysis (see below).

The global G_{ST} value was extremely low (0.001; Table 2) compared to other northern crab populations (0.031, Beacham et al. 2008; 0.011, Puebla et al. 2008), and Jost's (2008) measure of true differentiation (D) based on effective alleles was equally low (0.004; Table 2). These low values were driven primarily by the EBF sampling site, which showed significant linkage disequilibrium. Pairwise comparisons of G_{ST} values for all sampling sites with the exception of the EBF site were extremely low and resulted in no significant comparisons (Table 4). Furthermore, allele frequencies differed significantly (Fisher's method) at the EBF site from all other sites (Table 5). Pairwise D values were relatively low; however, the Beaufort Sea Pooled (BFP) region showed significant differentiation from a number of sites (Table 4), signifying that some genetic isolation may be occurring in the region. Nonetheless, allele frequencies, allelic richness, G_{ST} values, and the Bayesian analysis performed in STRUCTURE suggest that this structuring is weak (Tables 3, 4 and 5).

Meta-population structure and historical connectivity

Of the 60 samples randomly chosen for comparative analysis only a portion (44-49 per locus) were successfully genotyped by Canadian collaborators, largely due to poor DNA quality (Table 6). Consistency between labs in scoring of individuals ranged from 95.7% to 98.9% (Table 6). Scoring discrepancies were likely due to amplification artifacts and/or poor DNA quality. Average differences in raw allele scores for each locus were used, in conjunction with scatter plots of raw allele sizes from both datasets, to properly bin the alleles and ensure data compatibility. A total of 1504 samples (613 from the Alaskan region, 891 from the NW Atlantic) were successfully combined into one dataset and analyzed for population structure at 5 loci (*Cop2*, *Cop4*, *Cop3-4II*, *Cop24-3* and *Cop113*).

Table 4. Pairwise G_{ST} (top) and D (bottom) values for Alaskan region sampling sites. Negative values represented by zeros and bold values indicate significance after Bonferroni correction for multiple tests.

	PI	BR	SMI	CH	PH	CL	SWC	WI	NWC	NC	EBF	BC	BFP
BFP	0.0008	0	0.0011	0.0014	0.0017	0.0018	0	0	0.0015	0.0014	**0.0030**	0.0011	-
BC	0.0005	0.0016	0	0.0009	0	0.0009	0	0.0004	0	0	**0.0028**	-	**0.0397**
EBF	**0.0036**	**0.0024**	**0.0016**	**0.0030**	**0.0035**	**0.0026**	**0.0016**	**0.0026**	**0.0031**	**0.0024**	-	**0.0556**	**0.0685**
NC	0	0.0001	0	0.0006	0	0	0	0	0	-	**0.0598**	0	**0.0685**
NWC	0.0007	0.0009	0.0003	0.0013	0	0	0	0	-	0	**0.0729**	0	**0.0574**
WI	0.0018	0	0	0.0012	0	0	0	-	0	0	**0.0670**	0	0.0251
SWC	0.0009	0.0010	0	0	0	0	-	0	0	**0.0356**	**0.0578**	0.0062	0.0226
CL	0.0010	0	0.0004	0.0010	0	-	0.0121	0	0.0049	**0.0430**	**0.0659**	0.0282	**0.0706**
PH	0	0.0012	0	0	-	0	0.0140	0	0.001	0	**0.0849**	0	**0.0800**
CH	0.0006	0	0	-	0	**0.0357**	0	0.0097	0.0161	0.0222	**0.0560**	0.0092	**0.0485**
SMI	0.0008	0	-	0	0	0.0240	0	0.0034	0.0119	0.0097	0.0296	0	**0.0484**
BR	0.0016	-	0.0114	0.0006	0.0334	0.0104	0.0278	0	0.0256	0.0289	**0.0528**	**0.0361**	0.0085
PI	-	0.0197	0	0.0004	0	0.0267	0.0008	0	0.0057	0.0076	**0.0670**	0	0.0182

Table 5. Pairwise allele frequency comparisons for Alaska region. Significant *p*-values shown in bold.

	PI	BR	SMI	CH	PH	CL	SWC	WI	NWC	NC	EBF	BC
BFP	0.8939	0.8419	0.5986	0.2644	0.0668	0.2089	0.3899	0.8098	0.0980	0.0836	**<0.0001**	0.4106
BC	0.1352	0.0113	0.4189	0.2789	0.1240	0.0488	0.5002	0.4140	0.1903	0.9713	**<0.0001**	
EBF	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**		
NC	0.2757	0.1183	0.2242	0.0887	0.4318	0.0744	0.3670	0.3654	0.2454			
NWC	0.0358	0.1315	0.0635	0.0699	0.1229	0.5836	0.2852	0.7626				
WI	0.5051	0.7729	0.5364	0.4588	0.3569	0.9911	0.9141					
SWC	0.1008	0.0578	0.6772	0.4352	0.2451	0.6618						
CL	0.1776	0.7754	0.5532	0.3142	0.3061							
PH	0.5857	0.0230	0.4273	0.1052								
CH	0.3281	0.5500	0.9242									
SMI	0.3667	0.8039										
BR	0.0808											

Table 6. Scoring consistency (%) between laboratory groups analyzing the same samples for the purpose of dataset compatibility.

Locus	Number compared	Allele scoring consistency (% similar)
Cop2	48	95/96 = 98.9%
Cop4	48	92/96 = 95.8%
Cop3-4II	44	87/88 = 98.8%
Cop 24-3	49	95/98 = 96.9%
Cop113	46	88/92 = 95.7%

Snow crab from Atlantic Canada (AC) showed significant differentiation from snow crab in coastal Greenland (CG) as evidenced by allelic richness, overall gene diversity, and F_{ST} values at eight polymorphic loci (see Puebla et al. 2008). Thus, these two separate regions were treated as distinct populations in the large-scale analysis performed here. Crabs from the Alaska region (AR) were pooled into one population (AKP), with the exception of the EBF site, as it showed significant differentiation based on G_{ST}, D, and allele frequencies, likely associated with the described pattern of linkage disequilibrium. Analysis of the five loci across all Alaska and NW Atlantic sites resulted in global values of $G_{ST} = 0.017$ and $D = 0.127$ (Table 7). Significant divergence ($G_{ST} = 0.017$, $D = 0.196$; Fig. 8, Table 8) was found between CG and AC populations at a slightly lower, but similar magnitude to that reported by Puebla et al. (2008) ($F_{ST} = 0.027$), due to slight differences between software used and exclusion of three loci from the original study. Levels of divergence between AKP and CG populations were comparable to those between AC and CG, despite the increased geographic distance that separates the two regions (EBF $G_{ST} = 0.022$, $D = 0.240$, AKP $G_{ST} = 0.016$, $D = 0.204$; Fig. 8, Table 8). However, Alaskan crabs showed very low genetic differentiation from those in AC (EBF $G_{ST} = 0.007$, $D = 0.050$, AKP $G_{ST} = 0.003$, $D = 0.020$; Fig. 8, Table 8).

Table 7. Multi-regional analysis of observed heterozygosity (H_O); expected heterozygosity (H_S); G_{IT} (individual diversity relative to total diversity); G_{ST} (subpopulation diversity relative to total diversity); and Jost's measure of differentiation (D) (Jost 2008).

Locus	H_o	H_S	G_{IS}	G_{ST}	D
Cop2	0.825	0.831	0.008	0.0259	0.1451
Cop4	0.245	0.288	0.150	0.0219	0.0162
Cop3-4II	0.863	0.906	0.047	0.0123	0.1412
Cop24-3	0.896	0.924	0.030	0.0098	0.1515
Cop113	0.876	0.892	0.018	0.0167	0.1797
Overall	0.741±0.278	0.768±0.271	0.036	0.0173	0.1268

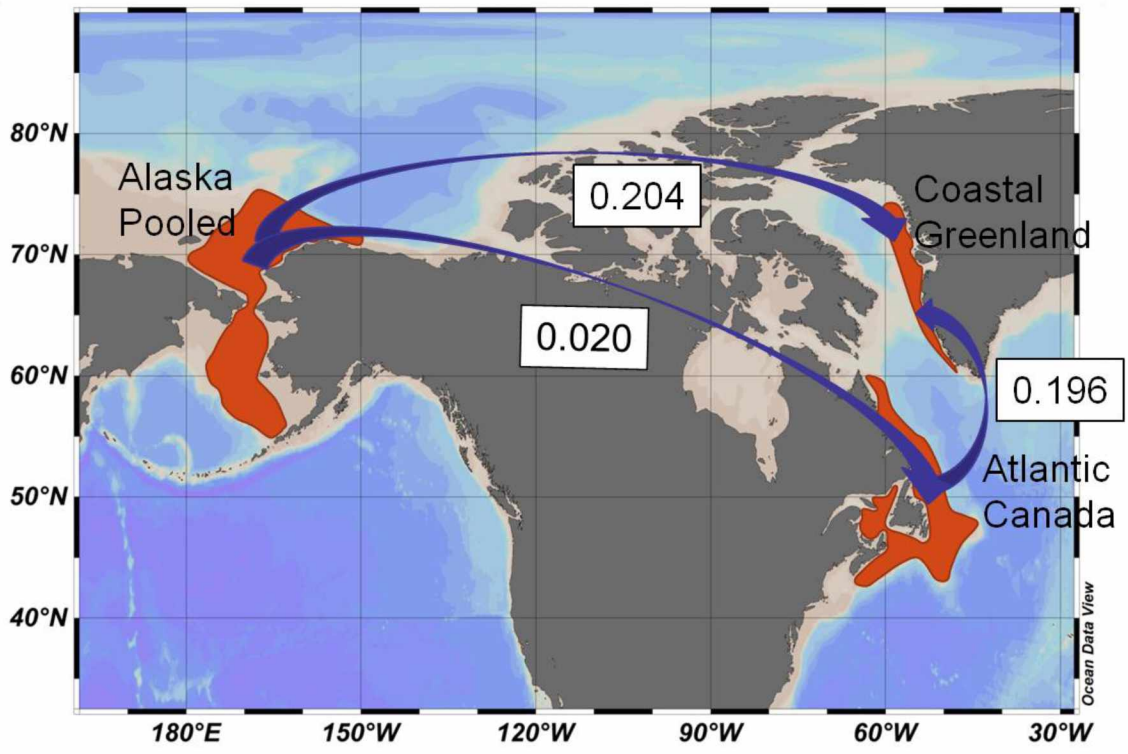

Fig. 8. Meta-population structure between Alaska (pooled sites), Coastal Greenland and Atlantic Canada sites, based on *D* (Jost 2008) values.

Table 8. Pairwise comparisons of regional groups for Jost's *D* (top) and G_{ST} (bottom). Values significant after sequential Bonferroni correction shown in bold.

	AKP	EBF	AC	G
AKP		0.0164	**0.0195**	**0.2039**
EBF	**0.0016**		**0.0502**	**0.2398**
AC	**0.0046**	**0.0073**		**0.1956**
G	**0.0164**	**0.0218**	**0.0166**	

The UPGMA tree illustrates the relatively low divergence between AC and Alaska Region (AR = AKP & EBF) crabs and the distance matrix shows that CG crabs are slightly more closely related to populations in AC than AR (Fig. 9, Table 8). Furthermore, 98.8% of alleles observed in CG crabs were found in AC, compared to 97.8% in the AR. 66.2% of alleles found in AC are present in CG and samples while only 65.2% of alleles from the AR are found there. These slight differences in allele frequencies add support to the argument of CG originating from AC; however, only slight differences in alleles exist between AC and AR (Table 9).

Estimates of *L(K)* indicated that values of $K = 1$ and $K = 2$ were the most likely, with the former slightly outranking the latter (-32060, -32200; Fig. 10). However, ΔK values suggested that K was most likely 2, given the magnitude of change between $K = 1$, $K = 2$ and $K = 3$ (Fig. 11). As discussed previously, ΔK for $K = 1$ cannot be computed; however, based on the rates of change between values of K, the largest change occured between $K = 2$ and $K = 3$, which would suggest 2 is the most likely value (Fig. 10). Differing results from each method made interpretation of K difficult and although the graphical representation of $K = 2$ (Fig. 12) showed that individuals within the Greenland population assign primarily to one cluster, membership of individuals from all other

populations appeared mixed. Interestingly, Alaskan and Atlantic Canada populations appeared to cluster together; however; the ability of STRUCTURE to properly assess

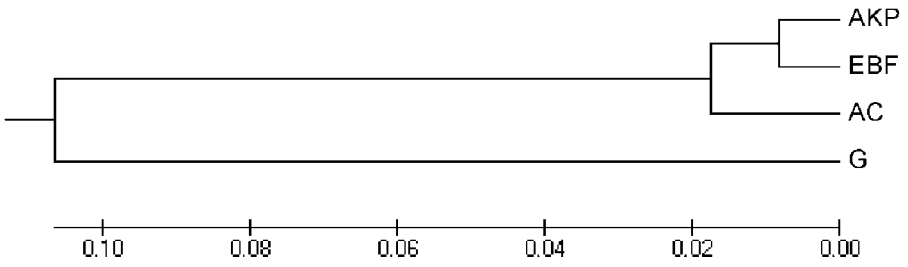

Fig. 9. Unweighted Pair Group Method with Arithmetic Mean (UPGMA) tree constructed from Jost's D values of genetic distance for regional group only.

Table 9. Population names and abbreviations for regional analysis data; (*N*) number of individuals sampled; (*A*) allelic richness over all loci and rarefied to the smallest sample size; (H_O) observed heterozygosity; (*alleles present*) percentage of shared alleles between populations.

Population	Abbr.	*N*	*A*	H_o	Alleles present
Alaska Region Pooled	AKP	573	13.5	0.869	97.8% of CG; 93.0% of AC
Eastern Beaufort Slope	EBF	40	11.1	0.873	
Atlantic Canada	AC	748	13.3	0.884	98.8% of CG; 92.5% of AKP
Greenland	G	143	11.0	0.849	65.2% of AR; 66.2% of AC
Mean			12.23±1.36	0.869±0.015	

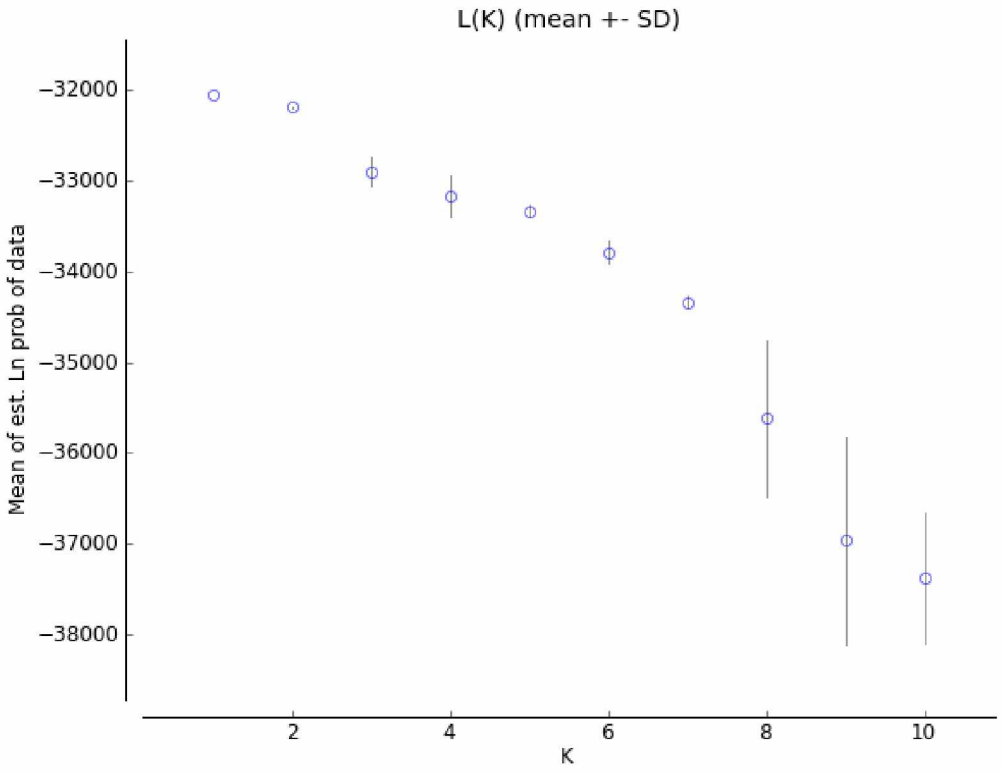

Fig. 10. Mean of estimated ln-likelihood probabilities for values of K (clusters) from 1 to 10 for regional analysis at 5 microsatellite loci. Probabilities were estimated using a Bayesian analysis method implemented in the program STRUCTURE and plotted using STRUCTURE Harvester.

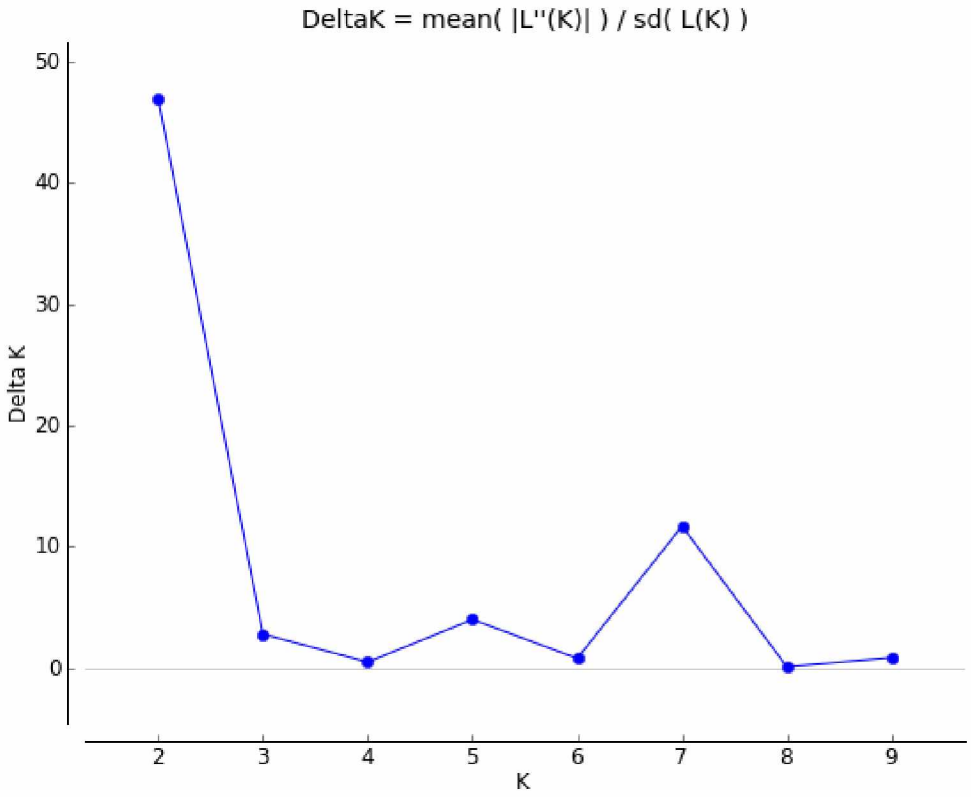

Fig. 11. Second-order rate of change (ΔK) for cluster values of 2-9 for regional analysis data generated from 5 microsatellite loci. Probabilities were estimated using a Bayesian analysis method implemented in the program STRUCTURE and plotted using STRUCTURE Harvester.

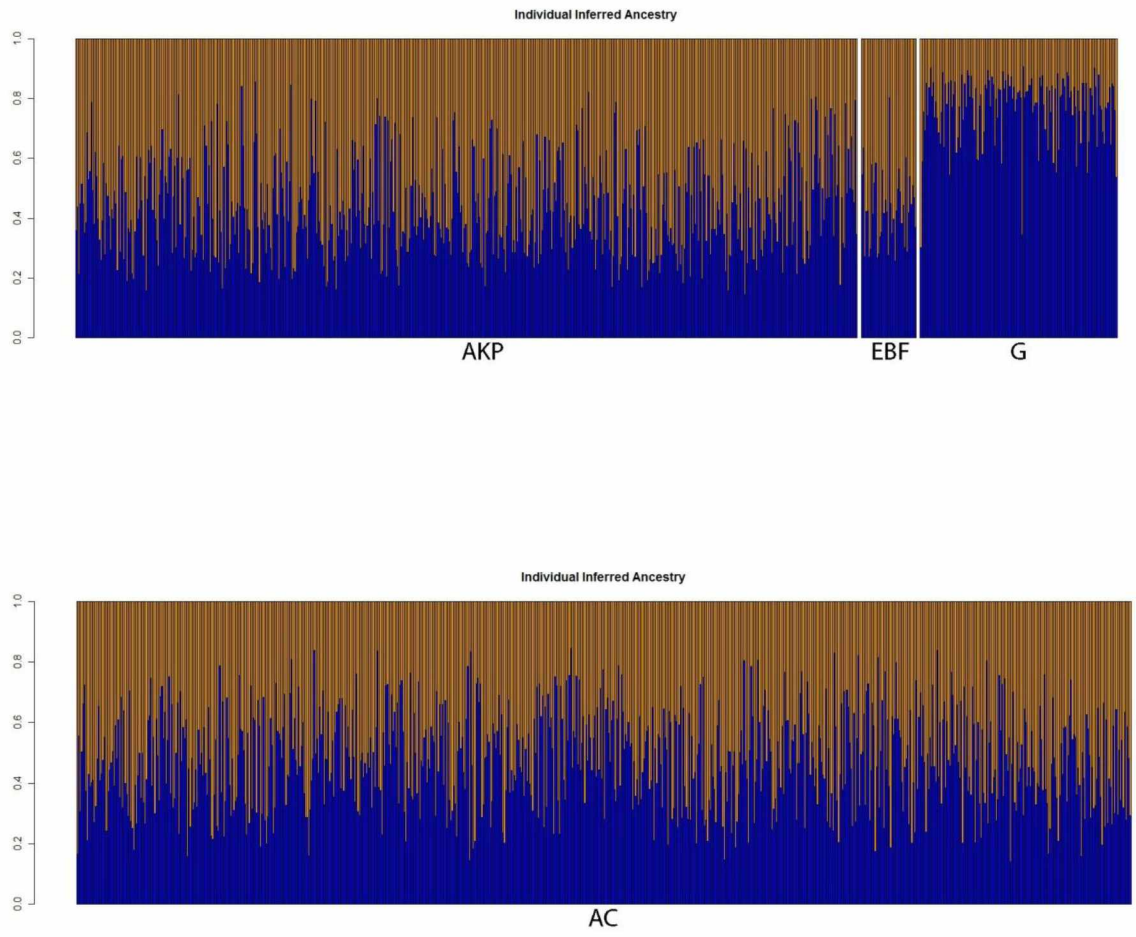

Fig. 12. Graphical representation of clustering from STRUCTURE for meta-population analysis. Each vertical line represents the probability that an individual's genotype corresponds to each cluster (*K* = 2).

population structure is low at F_{ST} levels <0.03 (Latch et al. 2006) and may be affecting these results.

Low differentiation between AR and AC populations points to recent gene flow between the two areas and/or large effective founding population size. Posterior probabilities of model scenarios generated in the program DIY ABC were attained by both the direct

estimate and logistic regression methods (Cornuet et al. 2008). Of the three historical scenarios explored, the scenario designating most recent gene flow at 3-5 ka had the highest posterior probability (logistic regression 89%; Table 10). Furthermore, in an evaluation of confidence in scenario choice performed in DIY ABC, 398 out of 500 (79.6%) bootstrap data sets generated had a larger posterior probability of scenario 1 than that of 2 or 3, making the probability of a Type I error 20.4%. Estimates of parameters under each scenario are summarized in Table 10.

Table 10. Parameters for modeled scenarios used in DIY ABC simulations. (DR PP) posterior probability estimates and 95% CI using direct rejection; (LR PP) posterior probability estimates and 95% CI using linear regression; (N_e) estimates of effective population size (95% CI); (t1,2,3) estimates of numbers of generations since last genetic exchange for each scenario (95% CI).

	Scenario 1	Scenario 2	Scenario 3
Model scenarios	N1 N2 0 sample 1 0 sample 2 t1 merge 1 2	N1 N2 0 sample 1 0 sample 2 t2 merge 1 2	N1 N2 0 sample 1 0 sample 2 t3 merge 1 2
DR PP	0.63 (0.54-0.72)	0.37 (0.28-0.46)	0.0 (0.0-0.0)
LR PP	0.89 (0.84-0.93)	0.11 (0.07-0.16)	0.0 (0.0-0.0)
N_1	73746	82176	86887
N_2	74381	84508	86836
t1	638		
t2		1567	
t3			21424

Discussion

Snow crab show a high level of genetic homogeneity throughout the Alaska region (AR) with the exception of the anomalous EBF site. Significant linkage disequilibrium at this site is likely a result of individuals from an unsampled population that differs in allele frequencies, being captured within the sample. The measures of differentiation employed here, however, suggest that the difference is significant, but subtle. Surprisingly, genetic homogeneity extends into the NW Atlantic as G_{ST} and D values are low between AR and Atlantic Canada (AC). Coastal Greenland (CG), however, does show significant differentiation from all other areas. It is likely that the long larval phase, long-distance adult migrations, and relatively short generation time (4.5-7.5 years; Alumno-Bruscia and Sainte-Marie 1998, Kruse et al. 2007) are responsible for genetic homogeneity within the AR. Low trans-Arctic divergence may be explained by a recent population expansion into the NW Atlantic since the last glacial maximum [LGM; 21,000 years ago (21ka); Miller et al. 2010]. A large effective founding population, in this case, would cause the forces of genetic drift to work slowly among AC crabs. Expansion of snow crab from the Bering Sea into the Chukchi and Beaufort Seas following the LGM may also provide an explanation of low divergence, and a similar phenomenon has been proposed in EBS red king crab (Grant et al. 2011).

Genetic population structure in Alaskan snow crab

The inability of STRUCTURE to detect multiple clusters within the AR is not surprising given that the algorithm implemented within the program designates population groupings in a way that minimizes linkage disequilibrium (LD), which was found at the most divergent sampling site (EBF). Furthermore, the low G_{ST} values found within the region represent population structure below levels at which the program can consistently detect structure (F_{ST} = 0.03; Latch et al. 2006). Population structure below this threshold can certainly be ecologically relevant, particularly when G_{ST} is affected by high heterozygosity. Here, however, the consensus of all ecological measures employed points

to low structuring, likely due to oceanographic flow that carries larvae primarily northward.

Significant Jost's D values were found at BFP (Table 4); however, all other divergence measures employed here do not suggest any differentiation at this location. Two sites from the Chukchi Sea as well as the two most geographically distant Bering Sea sites show no significant differentiation from BFP. Thus, these D values are unlikely to be ecologically relevant. Significant pairwise comparisons of Jost's D were found at three additional sampling sites (CL, NC, BC; Table 4); however, this pattern was not supported by multiple measures, and the spatial distribution of these sites does not indicate an ecologically relevant pattern such as a distinct stock. Significant pairwise allele frequency differences, G_{ST}, and D values all suggest that the EBF sample differs significantly in its genetic identity, and is possibly a distinct group of individuals (Tables 4 and 5). However, evidence for significant LD at this site warrants further investigation.

While significant LD tests can indicate lack of independence of genetic markers, true linkage has been ruled out here based on the finding that significant tests were not randomly distributed throughout the dataset. A bias in genotyping is also unlikely due to the scoring protocol implemented. All Beaufort Sea individuals were scored as a pooled sample, out of which subpopulations have not yet been defined. Other explanations for significant LD include: 1) a historical population bottleneck; 2) the collection of closely related individuals (i.e., brothers/sisters); 3) recent immigration from a distinct population not sampled here (admixture).

A historical bottleneck selects a small proportion of genotypes from the entire pool at random. Thus, the frequency of some haplotypes may appear in proportions greater than would be expected under an equilibrium scenario. However, tests for heterozygote excesses in Alaskan snow crab (Table 3) showed no evidence of historical bottlenecks. Furthermore, tests for heterozygote excess in BOTTLENECK and the calculation of the M-ratio indicate no such event. Similarly, sampling of closely-related individuals may also

produce haplotype frequencies different than expected under random sampling due to the inheritance of a small number of genotypes from similar parents. However, tests for relatedness also showed no evidence of familial relationships among sampled individuals (data not shown). Admixture thus seems the most likely explanation of genetic distinctness at EBF, given the ecological and environmental setting at this particular site. A newly admixed group could contain unique genotypes from each contributing population and the absence of heterozygous genotypes expected from random mating. Alternatively, a similar pattern may result if mating were occurring between admixed groups, but offspring were not recruiting back into either population. A local recruitment event would, in theory, break down the LD pattern by 50% per generation (Frankham et al. 2002).

Snow crab are known to migrate into deeper waters with ontogeny to form aggregations and mate (Ernst et al. 2005). All crab (36 males, 4 females) collected at the EBF site were morphometrically mature. The EBF site is located in 320 m of water and represents the northernmost observation of snow crab in the Beaufort Sea (Bluhm et al. 2005, Rand and Logerwell 2011). The Beaufort Sea experiences both eastward and cross-shelf (northward) flow (Garrison and Becker 1976, Pickart 2004), which could act to transport larvae into the inhospitable Canada Basin or the Eastern Beaufort shelf, where snow crab have not been documented. Although surrounding samples (BFP) show slight differentiation (Table 4), it is likely that the genetically divergent population required for this scenario may have originated outside the sampling area, such as the Mackenzie River Delta area, where historical (1963 only) snow crab presence has been recorded (Atkinson and Wacasey 1989a) and may be ephemeral.

To further test the likelihood of this scenario, 20 randomly selected individuals from Greenland (found here to be significantly divergent from Beaufort Sea crabs) were grouped with 20 randomly selected individuals from EBF and tested for LD. This exercise produced no significant LD results (data not shown); however, the population assumed to be contributing migrants to EBF could differ more significantly than the

Greenland population and thus send a stronger signal detected by the LD tests. Bayesian clustering failed to separate out individuals from within the EBF sampling site; however, the algorithm implemented in STRUCTURE works to minimize LD when creating clusters. In theory, a mating population that does not experience self-recruitment, but is a sink of individuals from surrounding areas, could be exploited with little consequence to future recruitment. However, sampling further to the east would help to confirm this hypothesis. Evidence here does not suggest that the significantly larger sized crabs found at BC or EBF are all from a separate genetic stock, so it may be possible that exposure to warm water, known to occur at depth in the area (Pickart et al. 2005), may be responsible for the larger size of these crabs.

Management implications

In contrast to snow crab, populations of Tanner and red king crab show evidence of divergence between Southeast Alaska, Gulf of Alaska, and Bering Sea regions and even within the EBS (Tanner crab only) (Bunch and Highsmith 1998, Merkouris et al. 1998, Grant et al. 2011). Regional separation is thought to be caused by oceanographic barriers created by the Aleutian Island chain and the southeast Alaskan archipelago; however, population structure of Tanner crab within the EBS is relatively unexplained (Merkouris et al. 1998). Currents and spawning site fidelity may be responsible, although Merkouris et al. (1998) found no evidence of population structure in EBS snow crab. Therefore, snow crab harvest is currently tracked in the eastern and western EBS subdistricts, but as opposed to Tanner crab, the units are not managed separately. It is possible that local currents contributing to EBS Tanner crab divergence may not affect snow crab, which do not occur as far into Bristol Bay as Tanners.

It is unlikely that distinct snow crab population units remain undiscovered within the Alaskan region, given the spatial coverage of sampling achieved here relative to the potential larval dispersal distances, migration capabilities, and modeled recruitment dynamics (Ernst et al. 2005, Parada et al. 2010). Although recruitment of larvae from the

Bering Sea into Arctic regions likely occurs, observations from this study and others (Paul et al. 1997, Bluhm et al. 2009) indicate reproduction is also occurring within the Chukchi and Beaufort Seas. Moreover, estimated residence times for water masses in the Chukchi Sea are sufficiently long to allow for local larval settling (Winsor and Chapman 2004).

The absence of a strict source-sink relationship between regions suggests Arctic stocks could persist even if population declines in the Bering Sea (NPFMC 2010) continued. Furthermore, the lack of isolated or distinct sub-populations should convey some resistance to population collapse due to apparently high migration and dispersal capabilities. Nonetheless, effects of harvest, disease, and climate change in the Bering Sea fishery area may adversely affect larval supply to "downstream" populations. However, populations with numerous distinct units are also thought to be more resilient than panmictic populations due to increased diversity (Schindler et al. 2010), so panmixia may be a detriment under some circumstances.

Management of the EBS snow crab stock as a panmictic unit is validated here as no distinct sub-populations were identified. Samples from the southernmost portion of the region (PI) do not show a reduction in genetic diversity or allelic richness, which would indicate that some connectivity in a southward direction is likely occurring. Arctic snow crab should be treated as highly connected stocks that are likely receiving more recruits from southern populations than they provide, based strictly on oceanographic flow and migration. One population in the Beaufort Sea showed significant divergence and lower (although non-significant) allelic richness than all other populations, indicating that a separate stock may be present. As a conservative measure, the groups of harvestable-sized crabs found in the Beaufort Sea should be managed separately from all other crab stocks.

Trans-Arctic exchange and historical connectivity

Snow crab are thought to have originated over 4 million years ago (Azuma et al. 2011). All six species of *Chionoecetes* are found in the Pacific whereas only *C. opilio* is found in the Atlantic, suggesting a Pacific radiation and a historical trans-Arctic expansion. Movement of snow crab into the NW Atlantic from the Pacific likely occurred in recent times by a large number of crabs, due to the low divergence found between the AC and AR meta-populations (Table 10). Higher levels of divergence that characterize the CG population are likely due to the effects of a smaller founding size, which caused genetic drift to work more quickly. Trans-Arctic connectivity most likely occurred since the LGM as warmer conditions may have favored snow crab presence throughout the Arctic.

Low genetic divergence between snow crab in the AR and AC was first evidenced from allozyme data by Merkouris et al. (1998). Confirmation of this trend by microsatellite analysis is still somewhat surprising, given the large geographic distance separating the populations and the apparent absence of snow crab through the Canadian Arctic Archipelago (CAA). However, strong genetic divergence is observed between CG crab and all other populations, indicating that the markers used here are effective in detecting population structure in this species. Therefore, the genetic homogeneity between AR and AC crabs must be due to recent/ongoing gene flow and/or an extremely large founding population size that has caused the forces of genetic drift to work slowly.

Although only a small number of trawls have been conducted throughout the CAA, snow crab are reported to be absent east of the Mackenzie River Delta and north of 56° N in NW Atlantic Canada and 74° N along the Greenland coast (Atkinson and Wacasey 1989b, Burmeister 2002, B. Sainte-Marie, Maurice Lamontagne Institute, Fisheries and Ocean Canada, Mont-Joli, Quebec, personal communication, 2011). Reasons for absence of snow crab throughout this region are not well understood as the species shows high tolerance for extreme cold water and does not appear to be subject to the narcotizing effects of magnesium in cold temperatures, which limit dispersal abilities of many

decapod crustaceans (Frederich et al. 2001). Benthic temperatures in parts of the CAA remain cold (<-1°C) year-round due to the absence of warmer Atlantic water at shallow depths, but more importantly year-round sea ice throughout the region limits warming of surface waters (Thomson 1982, Jones et al. 2003). It is thought that larval snow crabs may not be able to survive in surface waters colder than 8-10°C (Kon 1980, Kogane et al. 2005), which may explain their absence in colder regions. Snow crab are only present up to 60° N along the west coast of Baffin Bay, but occur up to 74° N along the E coast of Baffin Bay where the warmer east Greenland current persists, providing further evidence for temperature-limitation of the distribution (Squires 1990, Burmeister 2002). In addition, year-round sea ice presence in many areas may cause interannual variability in vertical carbon flux, (Dyke et al. 1996, Carmack and MacDonald 2002) resulting in food-limitation that may exclude snow crab from the CAA.

Historical climate data based on ice cores, pollen records, and radio carbon dating of fossilized bowhead whale (*Balaena mysticetus*) remains suggest that a number of warmer-than-present time periods have occurred in the CAA throughout the Pleistocene and Holocene (Dyke et al. 1996, Andreev et al. 2002, Miller et al. 2010, Polyak et al. 2010, Sundqvist et al. 2010). In considering a scenario of recent expansion of snow crab into the Arctic and NW Atlantic following the last glacial maximum (18 ka), data from bowhead whale remains in particular reveal a fine-scale sea-ice record. For the last 3,000 years (with the exception of very recent events) sea ice has failed to clear from the channels of the CAA during summer "flushing" of the Arctic, resulting in separation of Pacific and Atlantic bowhead stocks. Prior to that time, however, bowheads occupied these relatively ice free channels during at least two periods (3-5 ka and 8.5-10.5 ka) (Dyke et al. 1996). These ice-free periods may also have been more hospitable to snow crab larvae and provided migrational opportunities for adults.

If snow crab were present in AC prior to the LGM, they would likely have been forced into separate Atlantic and Pacific refugia during ice advance (cf., Maggs et al. 2008), which could have reduced effective population sizes through a bottleneck event. Under

this scenario, AR and AC crabs would likely show much higher divergence than currently seen due to genetic drift associated with the reduction in population size. Conversely, southward range shifts could have occurred with limited population size reduction or increases in rates of genetic drift due to the long-distance dispersal capabilities of the species. Therefore, I tested scenarios involving isolation both prior to and after the LGM.

The posterior probabilities for historical scenarios 1 and 2, which model connectivity since the LGM are far greater than that of scenario 3, which models connectivity prior to that time (Table 10). Although a number of taxa exhibit evidence of trans-Arctic exchange throughout history (reviewed in Hardy et al. 2011), Holocene events are recorded in marine taxa including sea grasses (*Zostera marina*), urchins (*Strongylocentrotus pallidus*), and bowhead whales (Palumbi and Kessing 1991, Dyke et al. 1996, Olsen et al. 2004). The estimates of effective population sizes (AC N_e = 65k, AR N_e = 70k) seem large enough to have slowed genetic drift over the last several thousand years, yielding low levels of divergence observed here. Furthermore, with estimates of mature male crabs in the Bering Sea and Gulf of Saint Lawrence well into the 100 millions (Moriyasu et al. 1998, NPFMC 2009), these effective population sizes are not unlikely over the areas sampled for this analysis.

Actual population size estimates for CG snow crab are smaller than EBS and AC stocks (ICES 2007). Therefore, a smaller effective founding population size is likely to have been present in the CG population, which would account for the higher level of divergence from AC and AR stocks. Due to the collective presence of all alleles found within the CG region, within both AR and AC populations, we can conclude that CG crabs were founded by one of these two populations recently, as opposed to prior to the LGM. Allele frequencies suggest a slightly closer relation of CG crabs to AC crabs; however, the overall difference between AC and AR crabs is relatively low.

Conclusions and future research directions

The Arctic is currently faced with a warming trend (Grebmeier et al. 2006) that may allow for increased resource extraction, both in the form of oil and gas developments in snow crab habitat, and in establishment of Arctic crab and other fisheries. Here, I find that relatively low genetic structuring of snow crab occurs throughout the Alaskan region, which demonstrates a high level of dispersal and connectivity within the species. Although population structuring can be important to maintaining healthy diversity within a species (Schindler et al. 2010), the panmictic nature of snow crab within this region is an indication of the species' ability to recolonize areas that have seen declines. Furthermore, no genetically isolated populations were identified within current fishing areas, indicating that current management procedures are appropriate. Some questions remain surrounding the Beaufort Sea populations, where commercial-sized crabs occur; however, further sampling over time and to the east may reveal the origins of the distinct (as-yet unsampled) population and whether or not the ecological dynamics are recurrent. Although cumulative evidence for relatively high gene flow within the Alaskan region is compelling at this point, the use of more advanced genetic markers such as Single Nucleotide Polymorphisms (SNPs) will help reduce genotyping errors and possibly increase resolution.

Meta-population analysis has revealed that colonization of the NW Atlantic by snow crab likely took place since the LGM; analysis of mitochondrial DNA, additional microsatellite loci, and/or SNPs may be able to provide additional support for this argument. Analysis of samples from Japanese, Siberian, and the recently-established Barents Sea populations of snow crab would offer a comprehensive picture of global snow crab connectivity, and may provide further insights into the historical glaciation events and population expansion/contraction in the Pacific. Investigating the southern-most ranges of the species may reveal increased genetic diversity, in the event that these areas were used as refugia during the LGM (Hewitt 1996, Hewitt 2004). Further investigations using Approximate Bayesian Computing may be used to determine

comprehensive population history as well as the temporal emergence of Greenland and Barents Sea populations.

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